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FINAL REPORT TO THE PAYETTE NATIONAL FOREST

ON

EFFECTS OF FIRE ON AQUATIC ECOSYSTEMS IN THE FRANK CHURCH - RIVER OF NO RETURN WILDERNESS DURING 1988

G. Wayne Minshall, Christopher T. Robinson, and Deron E. Lawrence

Stream Ecology Center
Department of Biological Sciences
Idaho State University
Pocatello, Idaho 83209

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PREFACE

Although resource managers periodically recognize the need for information on the effects of fires on stream fish habitat, the amount of research on the topic is amazingly sparse. The reasons include the sporadic nature of fires, the tendency to treat fires as short-term crises rather than regularly recurring phenomena, and short-comings in the organization (including the frequent transfer of personnel) and funding of government agencies responsible for watershed management. In addition, most of the published considerations to date of the effects of fire on stream ecosystems suffer from the lack of a long-term temporal perspective.

In 1979, following the 26,000 ha Mortar Creek Fire in central Idaho, we began a study to document the changes induced by wildfire on streams of various sizes in the Salmon River basin of the Frank Church "River of No Return" Wilderness. The purpose of this report is to compare results obtained during the first year (1979-1980) following the Mortar Creek Fire with those obtained in 1988. In addition, we deemed it essential to document conditions in a number of unburned wilderness streams within the Payette Forest in order to provide a point of reference against which to evaluate future changes due to fire (or other environmental perturbations). To achieve this second goal we examined an array of streams of different sizes within the Big Creek drainage. Although the results are presented within the context of a hypothesis concerning the role of habitat heterogeneity in the structuring of stream benthic macroinvertebrate communities, they also provide the desired baseline measures. The latter point is illustrated by the fact that soon after our study was conducted (August 1988) the Golden Fire (September 1988) burned about 7800 ha within and immediately adjacent to the Big Creek basin, including the watershed of one of our study sites (Cliff Creek).

For purposes of clarity and ease of presentation, the results of our studies are presented as two separate sections dealing with the Mortar Creek Fire and Big Creek, respectively.

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INTRODUCTION

Wildfires and some prescribed fires result in large, intense, uncontrolled, forest stand-replacing burns. Such fires instantly kill most above-ground vegetation, vaporizing much organic matter, and temporarily removing the protective cover from the soil. Forest regeneration following intense ("hot", crown) fires seems to follow one of several pathways depending on the soil-moisture regime and fire-return frequency (Schimpf et al. 1980, Arno et al. 1985). But, regardless of the particular sequence, the process requires 30 to 300 years to complete (Romme 1982, Lyon 1984, Arno et al. 1985). It is now generally recognized that stream ecosystem responses are closely linked to terrestrial plant conditions in the surrounding watershed (Ross 1963, Hynes 1975, Minshall et al. 1985). Therefore, changes in the structure and composition of terrestrial vegetation following intense fire may be expected to be reflected in the adjacent streams (Minshall et al. 1989). Since forest regeneration following intense fire is a long-term process, stream ecosystems may be expected to respond similarly and to shift in concert with temporal changes in plant structure (bare ground, shrub/herb, sapling, pole, mature forest, old growth forest) and species dominance.

Little scientific information currently is available on the effects of intense fires on streams in general and Rocky Mountain coniferous forest streams in particular (Tiedemann et al. 1979). Although several studies have been conducted into the effects of fire on water, most of these have focused on the short-term loss of nutrients from the land as detected in an aqueous carrier. Only two investigations (e.g. Johnson and Needham 1966, Albin 1979) have centered on the impact of fire directly on the stream ecosystem or specifically on the benthic invertebrate and algal communities.

The Mortar Creek Fire on the Middle Fork of the Salmon River, Idaho, (a National Wild River) began as an abandoned campfire on July 25, 1979, and by the time it was declared out on August 20, it had burned over 26,000 ha in the River of No Return Wilderness Area. Covering an area even larger than the state of New Hampshire, the Mortar Creek blaze was one of the largest in the Intermountain Region in this century. Studies conducted by the Stream Ecology Center at Idaho State University documented conditions in the first year following the fire (Minshall et al. 1981).

Although there are other fires of recent vintage in the Rocky Mountains, the Mortar Creek sites offer the advantages of (a) an intensive fire over an extensive area covering several watersheds and streams of different size, (b) known conditions immediately after the fire, (c) corresponding analyses from reference streams of similar size and landscape setting as the burn streams, and (d) location in a designated Wilderness Area with no major confounding anthropogenic disturbances.

The purpose of the study described below was to reexamine conditions in the Mortar Creek sites in 1988 in order to determine the kinds and magnitudes of changes which have occurred in the nine years following the fire.

STUDY SITES

A brief characterization of the streams utilized in this study is given in Table 1. Streams, both in burned and unburned watersheds, ranged from 1st to 5th order in size as determined from 7 1/2 minute USGS topographic maps. However, later direct verification indicated that Char Creek actually was a 2nd order stream. Streams in burned watersheds ("burn streams" for short) were comparable to their respective unburned "reference" stream in terms of external link and base flow, except that Marble Creek was about twice as big as Little Loon Creek. Location of sampling sites is given by the measurements of elevation and longitude and latitude as obtained from 7 1/2 minute USGS topographic maps.

Streams used for the study lie within the drainage of the Middle Fork of the Salmon River which flows through remote central Idaho within the River of No Return Wilderness Area. Access to the study sites is primarily by trail. The topography in this area shows high relief, with elevations ranging from 1220 m to 3150 m (Minshall et al. 1981). The geology of the area is comprised of Challis Volcanics (Eocene age) intruded by the Casto Pluton phase (Tertiary age) of the Idaho Batholith (Ross 1934). The climate in the area is semiarid, with most precipitation occurring in winter. Annual precipitation ranges from 38-100 cm depending on elevation (Minshall et al. 1981). Vegetation at the study sites includes: alder (*Alnus*), water birch (*Betula occidentalis*), black poplar (*Populus trichocarpa*), aspen (*Populus tremuloides*), and willow (*Salix*). Various conifer species are found in the moister areas of the adjacent slopes but rarely in high densities. These include: subalpine fir (*Abies lasiocarpa*), whitebark pine (*Pinus albicaulis*), Douglas fir (*Pseudotsuga menziesii*), and Ponderosa pine (*Pinus ponderosa*). The predominant shrub in the area is sagebrush (*Artemisia*).

METHODS

The variables selected for study and the type of sample [point (P), transect (T), or random throughout a lineal reach (R)] are indicated in Table 2. Emphasis was on biological responses, but key environmental factors expected to change as a result of fire also were included. Point sampling was used to obtain data specific to a given location or where one measurement was sufficient to characterize an entire reach. Transect sampling was used where factors were expected to vary across the stream in a regular manner. Random sampling was used where a number of samples were required to characterize an entire reach.

Most of the methods we used (Table 2) are routine in stream ecology and are described in detail in standard reference sources (Weber 1973, Greeson et al. 1977, Lind 1979, Merritt and Cummins 1984, APHA 1985). Further details are provided in the references in Table 2. Methods for sampling invertebrates are described in detail by Platts et al. (1983). Procedures for sample analysis also are outlined in Table 2. In addition to total standing crops, the invertebrate communities were examined in terms of

Table 1. Selected physical characteristics and locations of the Mortar Creek Fire Study sites.

STREAM	ORDER	LINK	BASE FLOW (m^3/s)	MBM* (cm)	ELEV (m)	LONGITUDE	LATITUDE
REFERENCE STREAMS							
TEAPOT	1	1	0.002	6	1390	115°02'37"	44°45'10"
PUNGO	2	10	0.04	8	1396	115°04'21"	44°45'56"
EF INDIAN	3	12	0.09	8	1413	115°05'32"	44°46'15"
INDIAN	4	89	0.31	9	1414	115°06'27"	44°46'02"
MARBLE	5	262	1.0	9	1344	115°01'00"	44°44'38"
BURN STREAMS							
CHAR	2	2	0.004	10	1356	114°56'08"	44°42'31"
LITTLE	2	7	0.07	10	1408	114°59'31"	44°43'11"
WFL LOON	4	24	0.10	10	1341	114°56'03"	44°42'35"
EFL LOON	4	105	1.5	14	1329	114°55'58"	44°42'35"
L LOON	5	132	2.0	12	1286	114°56'17"	44°43'45"

*MBM = Median Bed Material Size.

Table 2 SUMMARY OF VARIABLES, SAMPLING METHODS, AND ANALYTICAL PROCEDURES FOR EVALUATING THE EFFECTS OF WILDFIRE ON STREAM ECOSYSTEMS

VARIABLE	SAMPLE TYPE	SAMPLING METHOD	ANALYTICAL METHOD	REFERENCE
A. Physical				
1. Temperature (°C)	P	Maximun-Minimun recording thermometers.	Direct Observation	
2. Discharge (m^3/s)	T	Velocity-depth profiles.	Calculation: Q=w•D•V; where w=width, D=mean depth, and V=velocity.	Bovee and Milhous 1978
Width (0.1m)	P	Nylon-reinforced meter tape.	Determine width of water and bankful width.	Buchanan and Somers 1969
Depth (0.1m)	T	Meter stick.	Determine water and bankful depths at sufficient intervals to give a good estimate of the mean. No more than 10% of flow should pass between measurements.	
Velocity (0.1m/s)	T	Small Ott C-1 current meter.	Determine velocities at 0.6 x depth (from the surface) at sufficient intervals to give a good estimate of the mean. No more than 10% of the flow should pass between measurements. Estimate bankful velocities from Manning's equation.	Gregory and Walling 1973
3. Channel Gradient (%)	P	Inclinometer.	Measure water surface elevations over extended (150m) lengths upstream and downstream of the discharge transect.	
B. Chemical	P	"Grab" samples from center of stream.		
1. Alkalinity (mg/l)			Gran (in waters <40mg/l alkalinity) or methyl orange titration.	Talling 1973 APHA 1980
2. Hardness (mg/l)			EDTA titration.	APHA 1980
3. Specific Conductance (µmhos)		Determine in the field.	Temperature compensated portable YBI meter. Estimate total dissolved solids using standard conversion factor.	APHA 1980
C. Biological				
1. Periphyton	P/R	Collect samples from five separate cobblestones. Remove material from known area. Brush and rinse three times following prescribed technique. Collect material from each rock on a separate pre-combusted, tared, glass-fiber filter (Whatman GFF).	Acetone extraction of chlorophyll followed by spectrophotometric assay with correction for phaeopigments. Recombine acetone with sample and evaporate to dryness. Determine AFDM as described below.	Stockner and Armstrong 1971 Lorenzen 1966
2. Benthic invertebrates	P/R	Surber sampler fitted with 250 µm mesh net. Collect 5 samples per site in proportion to principal habitat types. Disturb substratum to depth of 10cm, remove all organic matter from larger inorganic particles, preserve in 5% formalin.	Separate invertebrates by species, count, dry at 60°C, and weigh. Determine population densities and biomass, species richness, dominance, diversity, and functional feeding group composition.	Platts et al. 1983 Merritt and Cummins 1984
3. Benthic organic matter	P/R	Recover from Surber samples described above.	Estimate percent composition of various plant components (including charcoal) dry at 60°C, ash at 550°C, determine total AFDM.	

P = point sample
R = random throughout a defined lineal reach
T = transect across stream

species richness, dominance, diversity, and principal functional feeding groups (Merritt and Cummins 1984, Cummins and Wilzbach 1985).

RESULTS AND DISCUSSION

Physical Changes of Streams

There appeared to be a decrease in % slope in the 1st and 2nd order burn sites (i.e. Char and Little Creek), which did not occur at the respective reference sites (Table 2). This response was not found in the larger burned-watershed stream sites. Greater maximum temperature differences also were found in these small headwater burn sites in the year following the fire. For example, Little Creek experienced a temperature maximum of 16 ^{o}C, whereas in the reference stream (Pungo Cr.) maximum temperatures reached only 11 ^{o}C (Table 3). Maximum temperatures returned to lower values by 1988 probably as a result of enhanced riparian conditions impeding sunlight. No differences in maximum temperatures were found in the larger streams.

Changes in Stream Channel Characteristics

Stream channel cross-sectional profiles remained reasonably constant in all reference streams between 1979/1980 and 1988/1989. However, they showed dramatic increases in depth and width at all of the burn sites over that same period (Figures 1, 2). West Fork Little Loon Creek had the greatest relative change and Little Creek the least.

Changes in Water Chemistry

Values of hardness, alkalinity, and specific conductance showed similar responses between burn and reference sites and between 1980 and 1988 (Table 4). Three different types of responses were found: (1) levels in reference and burn sites similar in 1980 and declining to comparable levels in 1988 (Teapot/Char, E.F. Indian/W.F.L. Loon), (2) reference and burn sites different in 1980 (by 12-16 units for hardness and alkalinity) declining to similar values in 1988 (Pungo/Little), and (3) burn site values about 2 x's higher than the reference site in 1980 and declining to substantially lower values in 1988, whereas reference sites remained about the same in the two periods (Indian/E.F.L. Loon, Marble/L. Loon). Thus, in three of the five cases the Mortar Creek Fire initially increased dissolved ion loads by substantial amounts but by 1988 these had returned to levels found in unburned streams. However, in two sets of cases, there was no apparent affect of the fire on water chemistry even though burn and reference sites both showed declines since the fire.

Changes in Periphyton

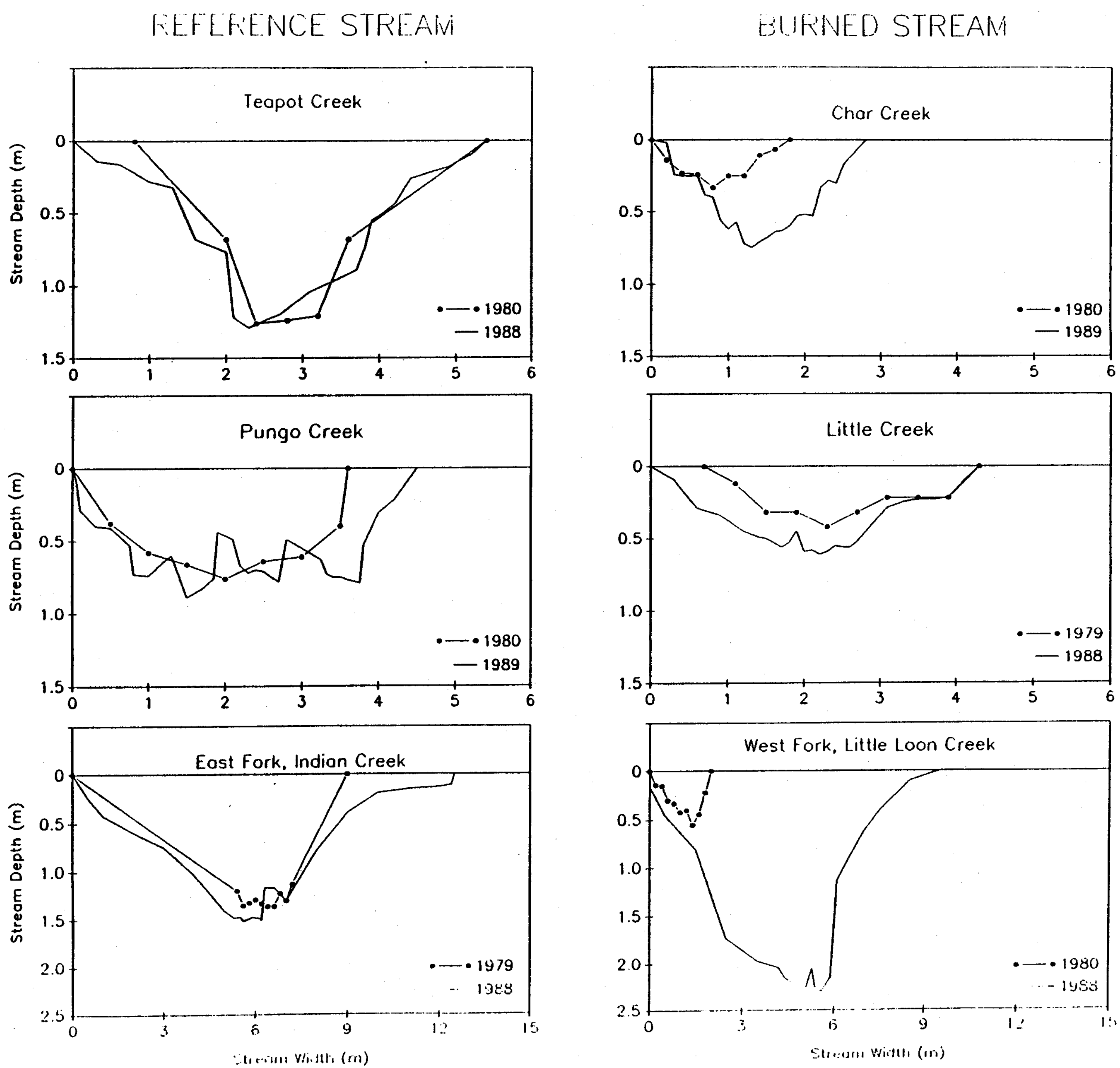
Streams were paired by size for comparisons. The primary response of periphyton in the 1st order stream (Char Creek) was the initial loss of moss. This is evident in the order of magnitude difference in chlorophyll a and AFDM levels in the reference stream (Teapot Creek) compared to Char Creek (Table 5). In addition, recovery by moss is not evident after 8 years, as is seen in the relatively low chlorophyll a and AFDM values for Char Creek in 1988 (Table 5). Little Creek, a 2nd order burn site,

Table 3. Percent slope and Delta ^{o}C (difference of maximum and mimimum temperature) for 1979 and 1987/1988 for the Mortar Creek Fire study sites. C=control sites, B=burn sites.

SITE	TYPE	%SLOPE		DELTA ^{o}C	
		1979	1987/88	1979	1987/88
TEAPOT	C	18	18*	7	7
CHAR	B	19	14	NA	10
PUNGO	C	7	7*	11	15
LITTLE	B	14	8*	16	12
EF INDIAN	C	4	5	NA	15
WFL LOON	B	9	9	15	16
INDIAN	C	2	3	16	NA
EFL LOON	B	3	4	NA	22
MARBLE	C	1	2*	NA	21
L LOON	B	5	4	18	21

*1987 year's data.

Figure 1. Channel profiles from permanent transects located within each study reach for the Mortar Creek Fire study sites for July 1980 versus July 1988. Burn sites are situated in the table adjacent to reference sites of similar size. In some cases 1979 or 1989 transect data was substituted for 1980 or 1988 transect data, respectively, due to erroneous transect placement for that particular study site.



REFERENCE STREAM
BURNED STREAM
Teapot Creek
1980
1988
Char Creek
1980
1989
Pungo Creek
1980
1989
Little Creek
1979
1988
East Fork, Indian Creek
1979
1988
West Fork, Little Loon Creek
1980
1988
Stream Depth (m)
Stream Width (m)

Figure 2. Channel profiles from permanent transects located within each study reach for the Mortar Creek Fire study sites for July 1980 versus July 1988. Burn sites are situated in the table adjacent to respective reference sites of similar size. In some cases 1979 or 1989 transect data was substituted for 1980 or 1988 transect data, respectively, because of erroneous transect placement for that particular site.

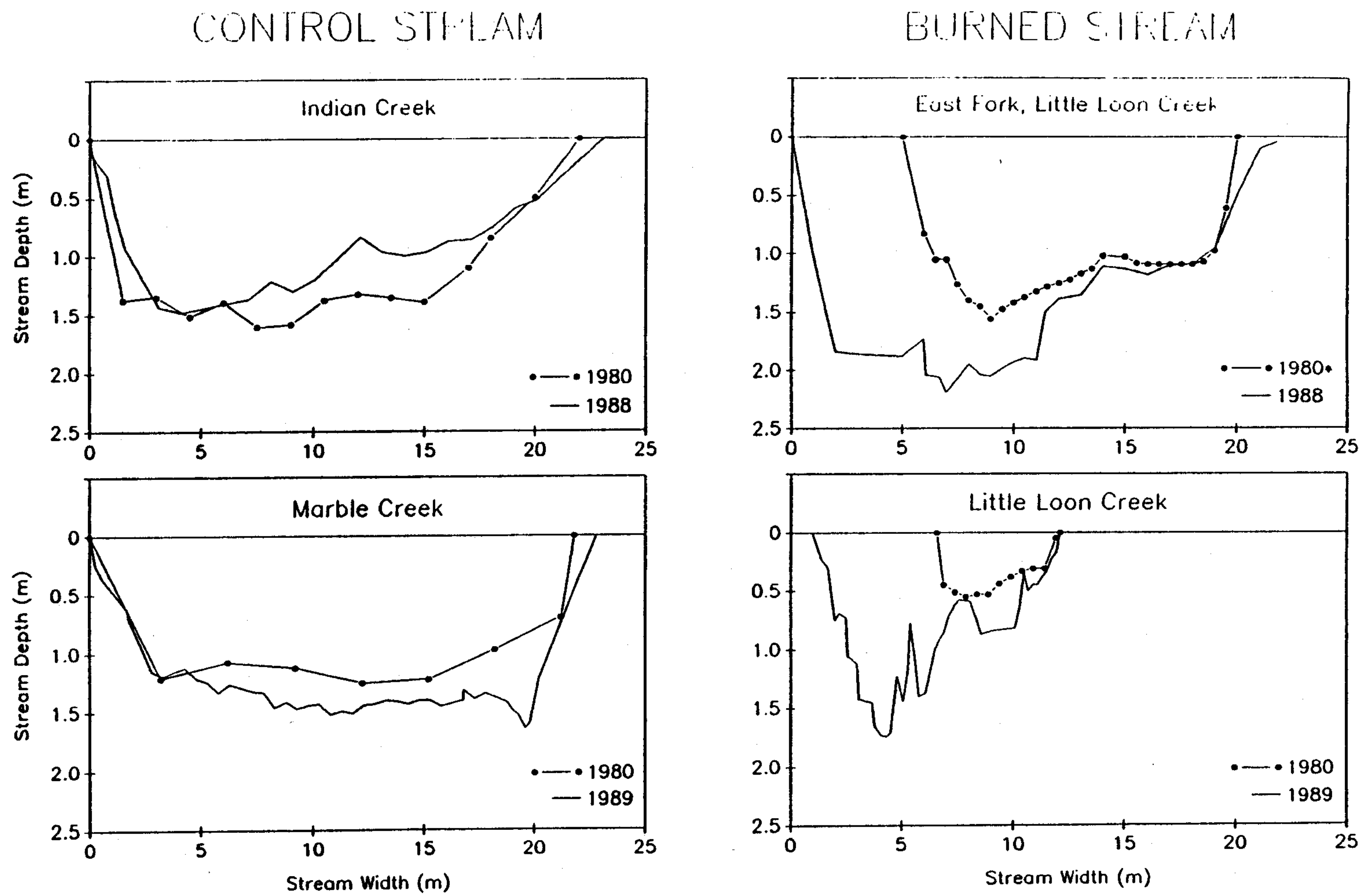

CONTROL STREAM
BURNED STREAM
Indian Creek
East Fork, Little Loon Creek
Marble Creek
Little Loon Creek
Stream Depth (m)
Stream Width (m)
1980
1988
1989
0
0.5
1.0
1.5
2.0
2.5
0
5
10
15
20
25

Table 4. Water chemistry for hardness (mg/l as $CaCO_3$), alkalinity (mg/l as $CaCO_3$), specific conductance (μmhos/cm at 25°C), and total dissolved solids (TDS; mg/l) for the Mortar Creek fire study sites. B=burn site, C=reference site.

STREAM	TYPE	HARDNESS		ALKALINITY		SPECIFIC CONDUCTANCE		TDS*	
		1980	1988	1980	1988	1980	1988	1980	1988
TEAPOT	C	26.7	19.2	39.3	21.1	92.6	47.8	60.2	31.1
CHAR	B	30.9	19.2	40.8	37.7	94.6	58.6	61.5	38.1
PUNGO	C	37.7	27.0	52.8	34.4	108.9	65.0	70.8	42.2
LITTLE	B	49.2	27.2	69.2	34.5	143.0	66.2	92.5	43.0
EF INDIAN	C	27.9	21.7	44.2	29.4	92.8	51.6	60.3	33.5
WFL LOON	B	39.4	19.1	48.2	28.9	102.4	54.4	66.6	35.4
INDIAN	C	21.7	22.4	34.6	30.5	77.2	77.0	50.2	50.0
EFL LOON	B	33.9	20.9	57.1	34.2	119.5	73.4	77.7	47.7
MARBLE	C	13.2	17.4	23.6	25.4	51.1	58.4	33.2	37.9
L LOON	B	32.5	20.1	55.8	32.1	121.1	49.6	78.8	32.2

*ESTIMATED AS 0.65X SPECIFIC CONDUCTANCE

Table 5. Periphyton chlorophyll a (ug/cm^2) and AFDM (g/m^2) values for July 1980 and July 1988 for the Mortar Creek Fire study sites. N=5 for each date and site. C=control sites, B=burn sites.

SITE	TYPE	CHLOROPHYLL a				AFDM			
		1980		1988		1980		1988	
		X	SD	X	SD	X	SD	X	SD
TEAPOT	C	33.6	15.3	12.8	10.5	18.6	8.9	28.2	22.7
CHAR	B	2.9	2.3	0.9	1.0	1.7	2.3	2.5	2.0
PUNGO	C	3.9	3.2	0.7	1.1	3.6	3.2	1.5	1.7
LITTLE	B	3.8	4.6	1.2	1.9	5.3	3.6	2.6	0.6
EF INDIAN	C	3.6	1.3	0.6	0.5	1.6	0.7	1.4	0.8
WFL LOON	B	2.1	1.1	2.7	2.2	4.6	1.5	7.0	6.1
INDIAN	C	9.6	5.5	1.0	0.6	6.2	3.4	8.0	5.4
EFL LOON	B	0.4	0.2	4.3	1.5	1.1	0.6	23.2	11.0
MARBLE	C	6.6	4.3	1.4	0.9	14.2	5.5	5.8	3.7
L LOON	B	1.2	1.5	1.9	1.8	1.8	0.6	5.4	3.5

displayed an initial increase in chlorophyll a and AFDM followed by a decrease in 1988. This trend would be expected in streams of this size due to enhanced riparian conditions over time impeding light from reaching the stream. Light intensity is important for periphyton development and production in streams (Towns 1981, Steinman and McIntire 1987). In the larger streams there was an initial decrease in periphyton in 1980 when compared to reference streams, followed by an increase in 1988. This trend is most obvious in E.F.L. Loon where chlorophyll a increased from 0.4 ug/cm^2 in 1980 to 4.3 ug/cm^2 in 1988 (Table 5). Enhanced riparian conditions that reduce light levels to streams may not be sufficient to impede periphyton development in larger streams (Vannote et al. 1980).

Changes in benthic organic matter (BOM)

Benthic organic matter dramatically increased in the burn streams in 1980, especially in the smaller (3rd order or less) streams. Organic matter in these smaller streams typically was 2-3x greater than in the reference sites (Table 6). By 1988 values of BOM were similar between burn and reference streams. Composition analysis of the BOM indicated that the increase in organic matter was due to the high input of charcoal in the burn streams. An anomaly exists in 1980 at Indian Creek and E.F.L. Loon Creek where the reverse trend is evident, although these sites also were similar by 1988.

Changes in Macroinvertebrate Community Structure

Community level indices. In general, the total number of organisms were lower in 1980 than in 1988 for all of the stream sites except for Char Creek. Char Creek had 3x the number of organisms than the reference stream (Teapot Creek) in 1980, whereas the number of organisms in these two streams were comparable in 1988 (Figure 3). The difference exhibited in 1980 between Char Creek and Teapot Creek may be due to habitat differences associated with the loss of moss in Char Creek. Teapot Creek exhibited the same general trend of increasing organism abundance from 1980 to 1988 as did all of the other sites (Figure 3).

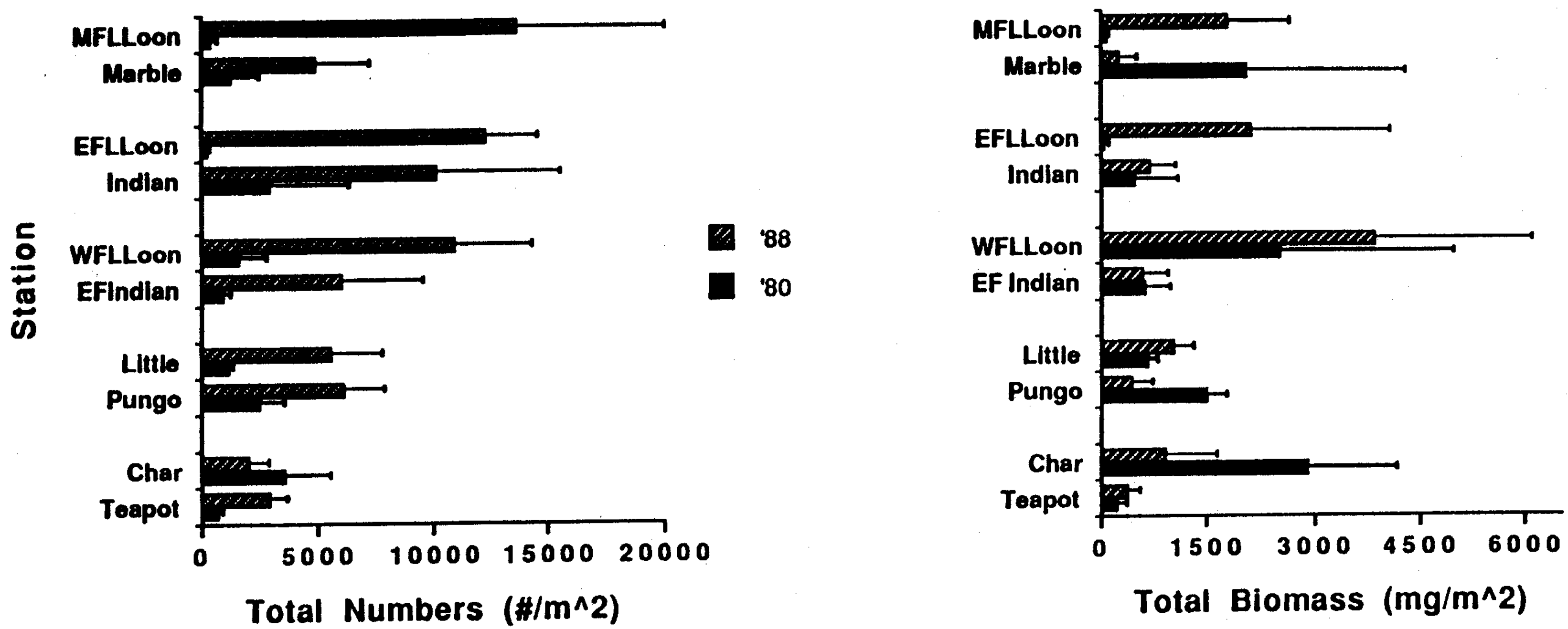
The total biomass of organisms was comparable between 1980 and 1988 for all reference streams except Pungo and Marble Creeks in which the biomass of organisms decreased by half from 1980 to 1988. In contrast, most of the burn streams displayed orders of magnitude increases in total biomass between 1980 and 1988 (Figure 3). Total biomass in Char Creek followed the trend of total numbers, decreasing from 1980 to 1988. The discrepancy between the numbers data and the biomass data between most burn and reference sites suggests possible subtle changes in insect life history in response to changes in habitat as a function of fire.

Species richness generally was higher in 1988 than in 1980 at both burn and reference sites (Figure 4). In 1980, species richnesses for East Fork and Main Little Loon were less than for the respective reference sites; at the other burned streams they were either equal to or greater than in the reference sites. In 1988, species richness was nearly the same for all burn and reference pairs except Little Loon/Marble. Shannon-Weiner diversities (Figure 4) showed patterns similar to those of richness except for Char/Teapot in 1980 where H' was lower at Char than at Teapot. The .rm80
reason for the low H' in Char Creek may lie in the species shift where, although the same species were present, most of them were chironomids.

Table 6. Benthic organic matter (BOM; g/m^2) and % charcoal associated with Surber samples taken in July 1980 and July 1988 from the Mortar Creek Fire study sites. N=5 for each site and date. C=control site, B=burn site.

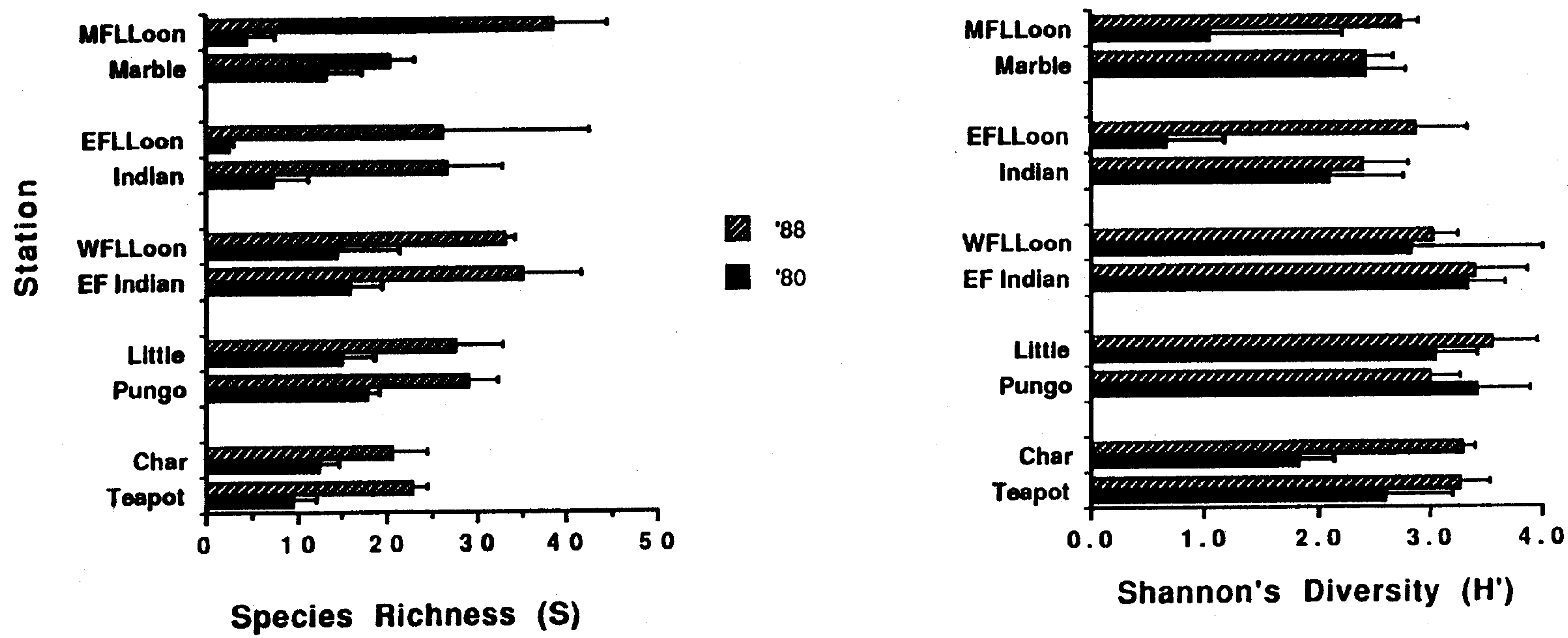
SITE	TYPE	BOM (g/m^2) 1980 X	BOM 1980 SD	BOM 1988 X	BOM 1988 SD	% CHARCOAL 1980 X	% CHARCOAL 1980 SD	% CHARCOAL 1988 X	% CHARCOAL 1988 SD
TEAPOT	C	20.9		15.0	6.9	6		8	10
CHAR	B	92.2		26.8	19.9	100		12	5
PUNGO	C	13.9		13.4	13.5	0		10	8
LITTLE	B	32.5		19.9	8.9	82		10	7
EF INDIAN	C	15.1		16.0	17.6	0		10	9
WFL LOON	B	59.7		10.6	6.9	58		9	10
INDIAN	C	59.3		8.8	2.6	0		16	13
EFL LOON	B	16.1		11.6	5.7	10		17	12
MARBLE	C	6.9		9.0	6.7	0		5	5
L LOON	B	21.5		7.3	0.9	0		8	3

Figure 3. Comparison of macroinvertebrate total numbers ($\#/m^2$) and total biomass (mg/m^2) for 1980 versus 1988 for the Mortar Creek Fire study sites. Burn sites are situated in the table above respective reference sites of similar size. N=5 for each site by year. Bars respresent ± 1 SD.



Station
MFLLoon
Marble
EFLLoon
Indian
WFLLoon
EFIndian
Little
Pungo
Char
Teapot
0
5000
10000
15000
20000
Total Numbers (#/m^2)
'88
'80
MFLLoon
Marble
EFLLoon
Indian
WFLLoon
EF Indian
Little
Pungo
Char
Teapot
0
1500
3000
4500
6000
Total Biomass (mg/m^2)

Figure 4. Comparison of macroinvertebrate species richness (S) and Shannon-Weiner diversity (H') for 1980 versus 1988 for the Mortar Creek Fire study sites. Burn sites are situated in the table above respective reference sites of similar size. N=5 for each site by year. Bars represent $\pm$1 SD.


Station
MFLLoon
Marble
EFLLoon
Indian
WFLLoon
EF Indian
Little
Pungo
Char
Teapot
0
10
20
30
40
50
Species Richness (S)
'88
'80
MFLLoon
Marble
EFLLoon
Indian
WFLLoon
EF Indian
Little
Pungo
Char
Teapot
0.0
1.0
2.0
3.0
4.0
Shannon's Diversity (H')

Functional Feeding Group Response. In 1980 an increase in the relative abundances of miners and a decrease in the relative abundances of scrapers and gatherers occurred in all burn sites when compared to reference sites (Table 7). Indeed, scraper absolute numbers were typically less than $100/m^2$ in burn sites, while ranging from 100 to over $900/m^2$ in reference sites (Table 8). The absolute and relative abundances of shredders and predators were similar between burn and reference sites in 1980, although Marble Creek had 100x as many shredders as the burn site (mainstem L. Loon Creek). Filterers were low in absolute and relative abundances in E.F.L. Loon Creek and mainstem L. Loon Creek in 1980 (Table 7, 8).

In 1988 most burn sites were comparable in functional feeding group relative abundances with their respective reference sites except for gatherers (Table 7). Gatherers tended to remain low in relative abundance in most burn sites in 1988. Scrapers increased in absolute and relative abundances in burn sites from 1980 to 1988, especially in terms of absolute numbers (Table 8). Miners decreased in predominance in burn sites to levels comparable with respective reference sites, although absolute numbers were higher (2-10x) in 1988 than 1980 for all sites. The absolute abundances of shredders were substantially higher in Little Creek over the reference stream (Pungo Creek) in 1988. Filterer relative abundance increased in W.F.L. Loon Creek from 1980 to 1988.

In terms of relative biomass, predators had similar levels in most burn versus reference sites and between 1980 to 1988 (Table 9). The relative biomass of predators was high in all sites for both 1980 and 1988, probably due to the relatively large size of predators. The absolute biomass of predators was substantially greater in Char Creek over Teapot Creek for both years (Table 10). Miners displayed low values of relative biomass as compared to relative numbers, although tending to increase in 1988 in most burn sites. Filterers followed similar trends between years for respective burn and reference sites, except Indian Creek which had a predominance of filterers in 1988. The relative biomass of filterers in E.F.L. Loon Creek decreased from 1980 to 1988, although their absolute biomass was substantially greater in 1988. Gatherers increased relative biomass values from 1980 to 1988 in the burn streams, although absolute biomass values were comparable between burn and reference sites in 1988 (Table 10). No obvious trends are evident in the relative biomass of shredders, although shredders increased in Little Creek in 1988. In addition, the relative biomass of shredders was higher in 1980 in E.F. Indian Creek and Marble Creek compared to respective burn sites. The absolute and relative biomass of scrapers was similar between burn and reference sites in 1988. As with relative numbers, the relative biomass of scrapers was higher in W.F.L. Loon Creek than in the respective reference site in 1980 (Table 9).

CONCLUSION

The data show substantial changes in abiotic and biotic variables for all sizes of stream ecosystem examined. Considerable recovery seems to have occurred within the first nine years. However the true extent of the damage and the degree of recovery would be more readily apparent if the time sequence of events incorporating each of the first ten years of change could be examined. These missing data are available, although mostly in raw form, and future efforts should be made to provide for their reduction, analysis, and synthesis. Although complete recovery to prefire conditions is believed to require considerable time (Minshall et al. 1989), this is the first study to examine a full suite of ecosystem-level parameters over even just a 9-year time span. Such information is essential for the development and implementation of an appropriate fire management policy and for the intelligent management of aquatic resources in wilderness areas.

Table 7. Relative abundances (as %) of macroinvertebrate functional feeding groups for the Mortar Creek burn (B) sites and reference (C) sites for 1980 and 1988.

Station			SCRAPERS X	SHREDDERS X	GATHERERS X	FILTERERS X	MINERS X	PREDATORS X
Teapot	**C**	**'80**	31%	24%	6%	2%	10%	26%
		'88	7%	6%	21%	15%	35%	16%
Char	**B**	**'80**	2%	19%	1%	1%	67%	9%
		'88	10%	18%	8%	10%	24%	27%
Pungo	**C**	**'80**	27%	4%	13%	0%	34%	22%
		'88	5%	3%	8%	26%	47%	12%
Little	**B**	**'80**	8%	10%	7%	3%	40%	33%
		'88	10%	18%	12%	6%	34%	19%
EFIndian	**C**	**'80**	52%	2%	10%	1%	7%	28%
		'88	14%	2%	29%	4%	34%	13%
WFLL	**B**	**'80**	41%	5%	6%	1%	29%	17%
		'88	21%	2%	2%	22%	42%	9%
Indian	**C**	**'80**	32%	0%	16%	42%	8%	1%
		'88	5%	2%	8%	3%	56%	26%
EFLL	**B**	**'80**	2%	0%	0%	2%	92%	4%
		'88	21%	1%	2%	11%	57%	7%
Marble	**C**	**'80**	9%	19%	3%	34%	28%	6%
		'87	7%	5%	4%	1%	71%	11%
MFLL	**B**	**'80**	5%	1%	2%	0%	89%	3%
		'88	19%	1%	2%	9%	65%	5%

Table 7. Relative abundances (as %) of macroinvertebrate functional feeding groups for the Mortar Creek burn (B) sites and reference (C) sites for 1980 and 1988.

Station			SCRAPERS X	SHREDDERS X	GATHERERS X	FILTERERS X	MINERS X	PREDATORS X
Teapot	C	'80	31%	24%	6%	2%	10%	26%
		'88	7%	6%	21%	15%	35%	16%
Char	B	'80	2%	19%	1%	1%	67%	9%
		'88	10%	18%	8%	10%	24%	27%
Pungo	C	'80	27%	4%	13%	0%	34%	22%
		'88	5%	3%	8%	26%	47%	12%
Little	B	'80	8%	10%	7%	3%	40%	33%
		'88	10%	18%	12%	6%	34%	19%
EFIndian	C	'80	52%	2%	10%	1%	7%	28%
		'88	14%	2%	29%	4%	34%	13%
WFLL	B	'80	41%	5%	6%	1%	29%	17%
		'88	21%	2%	2%	22%	42%	9%
Indian	C	'80	32%	0%	16%	42%	8%	1%
		'88	5%	2%	8%	3%	56%	26%
EFLL	B	'80	2%	0%	0%	2%	92%	4%
		'88	21%	1%	2%	11%	57%	7%
Marble	C	'80	9%	19%	3%	34%	28%	6%
		'87	7%	5%	4%	1%	71%	11%
MFLL	B	'80	5%	1%	2%	0%	89%	3%
		'88	19%	1%	2%	9%	65%	5%

Table 8. Absolute abundances (#/m^2) and standard deviations of macroinvertebrate functional feeding groups for the Mortar Creek burn (B) sites and reference (C) sites for 1980 and 1988.

		SCRAPERS		SHREDDERS		GATHERERS		FILTERERS		MINERS		PREDATORS	
		X	SD	X	SD	X	SD	X	SD	X	SD	X	SD
Teapot	C '80	223.8	73.5	170.0	125.3	45.2	36.8	17.2	12.3	75.3	53.8	191.5	173.6
	'88	181.4	92.8	168.6	48.0	627.4	369.2	510.0	577.2	979.5	417.2	456.7	169.7
Char	B '80	68.9	40.7	688.6	388.6	47.3	82.9	40.9	50.1	2362.9	1575.0	335.7	219.4
	'88	228.3	162.2	371.3	199.5	128.0	86.4	207.0	257.1	437.5	248.6	578.3	300.9
Pungo	C '80	660.7	125.2	109.8	57.6	327.1	177.9	8.6	4.8	835.0	898.1	550.9	247.4
	'88	273.2	71.5	189.9	95.0	450.3	196.3	1705.1	1284.7	2740.1	966.7	755.4	449.2
Little	B '80	86.1	22.8	109.8	44.0	81.8	101.7	34.4	56.1	458.4	111.5	374.5	90.5
	'88	582.6	284.9	1086.2	583.6	667.9	352.1	441.7	786.4	1845.9	1010.4	977.4	433.2
EFIndian	C '80	443.3	197.4	19.4	31.7	83.9	17.7	8.6	14.0	56.0	39.1	234.6	147.6
	'88	670.1	272.1	256.1	81.1	1606.9	829.1	262.5	242.2	2462.6	2201.2	796.0	555.9
WFLL	B '80	628.4	704.0	81.8	114.0	96.8	174.8	17.2	28.1	439.0	362.9	256.1	243.8
	'88	2317.5	1061.7	215.5	172.9	166.5	52.3	2466.9	2634.4	4349.1	2262.0	1094.7	792.8
Indian	C '80	934.0	1265.4	0.0	0.0	477.7	741.8	1235.3	1485.9	245.3	184.1	30.1	67.4
	'88	488.7	360.6	202.7	175.0	708.5	297.7	207.0	159.0	6011.5	3758.0	2501.0	1386.0
EFLL	B '80	4.3	5.9	0.0	0.0	0.0	0.0	4.3	9.6	170.0	151.1	6.5	5.9
	'88	2745.4	1622.9	163.3	141.9	293.4	72.6	1397.8	892.0	5441.7	3247.9	800.3	338.2
Marble	C '80	111.9	102.3	221.7	342.0	38.7	27.0	400.3	574.0	333.7	227.4	73.2	55.6
	'87	386.3	390.7	273.2	158.5	215.5	124.5	36.3	31.7	3465.6	1626.9	535.6	342.6
MFLL	B '80	19.4	22.1	2.2	4.8	6.5	5.9	0.0	0.0	318.5	322.1	10.8	13.2
	'88	2528.8	1076.6	91.8	75.8	185.7	109.9	1775.5	2814.7	8472.0	2948.1	584.7	237.9

Table 9. Relative biomass (as %) of macroinvertebrate functional feeding groups for the Mortar Creek burn (B) sites and reference (C) sites for 1980 and 1988.

Station			SCRAPERS X	SHREDDERS X	GATHERERS X	FILTERERS X	MINERS X	PREDATORS X
Teapot	C	**'80**	12%	24%	5%	7%	8%	44%
		'88	25%	11%	25%	4%	25%	29%
Char	B	**'80**	14%	18%	4%	28%	7%	28%
		'88	10%	11%	6%	11%	10%	52%
Pungo	C	**'80**	34%	5%	39%	4%	3%	16%
		'88	16%	3%	20%	2%	16%	43%
Little	B	**'80**	22%	9%	15%	19%	3%	32%
		'88	32%	24%	7%	3%	32%	19%
EFIndian	C	**'80**	38%	25%	3%	2%	1%	31%
		'88	10%	5%	31%	17%	10%	30%
WFLL	B	**'80**	52%	5%	6%	7%	13%	16%
		'88	11%	1%	3%	28%	11%	16%
Indian	C	**'80**	24%	0%	2%	0%	72%	1%
		'88	16%	4%	10%	27%	16%	30%
EFLL	B	**'80**	14%	0%	0%	44%	1%	41%
		'88	28%	3%	5%	25%	28%	16%
Marble	C	**'80**	10%	18%	7%	3%	57%	6%
		'87	9%	12%	13%	7%	28%	31%
MFLL	B	**'80**	19%	1%	7%	25%	0%	48%
		'88	34%	5%	3%	20%	34%	20%

Table 10. Absolute biomass (mg/m^2) and standard deviations of macroinvertebrate functional feeding groups for the Mortar Creek burn (B) sites and reference (C) sites for 1980 and 1988.

Station		SCRAPERS X	SCRAPERS SD	SHREDDERS X	SHREDDERS SD	GATHERERS X	GATHERERS SD	FILTERERS X	FILTERERS SD	MINERS X	MINERS SD	PREDATORS X	PREDATORS SD
Teapot	C '80	27.5	13.3	56.0	32.0	10.5	10.0	16.8	15.5	19.6	42.6	101.4	127.7
	'88	20.1	12.1	38.6	34.0	91.3	88.5	10.0	6.8	108.5	159.3	98.2	76.7
Char	B '80	420.9	585.6	538.6	411.4	124.0	76.7	808.1	409.1	199.9	165.5	820.3	260.3
	'88	53.4	31.8	100.4	69.5	24.5	10.6	87.5	83.9	53.2	30.1	562.8	548.3
Pungo	C '80	509.4	265.2	74.0	142.7	582.9	36.0	57.2	73.3	40.2	58.0	235.9	67.2
	'88	65.2	38.7	13.8	11.4	83.9	54.2	6.9	4.9	68.6	40.0	207.6	158.3
Little	B '80	141.0	97.6	59.4	65.9	100.5	92.5	127.4	128.6	17.2	36.7	209.2	54.4
	'88	161.8	124.3	257.6	144.6	72.6	56.6	31.7	62.2	296.6	117.0	190.7	117.3
EFIndian	C '80	236.9	183.2	156.7	346.7	16.4	17.6	11.0	8.4	7.1	14.7	192.4	166.2
	'88	52.1	29.3	19.2	23.5	173.7	85.0	111.9	116.3	67.2	68.7	169.9	129.6
WFLL	B '80	1301.7	1643.0	132.1	82.0	156.2	137.1	184.2	104.4	318.5	529.2	413.4	255.6
	'88	1525.3	1203.5	26.5	11.1	91.3	39.8	1181.6	942.4	360.2	197.4	530.6	346.0
Indian	C '80	116.9	165.4	0.0	0.0	9.9	5.8	0.9	0.5	345.6	459.2	4.3	9.6
	'88	74.4	38.2	24.4	28.5	64.7	15.4	148.6	84.6	106.8	55.0	260.5	306.2
EFLL	B '80	7.5	9.2	0.0	0.0	0.0	0.0	23.9	22.4	0.6	1.4	22.2	38.5
	'88	325.3	241.4	46.6	73.2	109.9	82.1	943.7	1634.4	394.8	219.4	202.0	173.1
Marble	C '80	195.8	383.7	358.7	670.8	133.2	169.1	63.9	72.6	1154.8	2399.4	117.7	147.4
	'87	38.3	69.0	19.2	6.0	26.1	18.6	14.3	11.8	56.4	36.7	103.9	149.4
MFLL	B '80	12.1	12.8	0.4	1.0	4.1	5.3	15.7	12.2	0.0	0.0	30.1	39.8
	'88	307.7	168.9	95.1	205.3	53.4	45.3	444.9	457.1	475.2	146.7	378.4	307.3

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II. LOTIC MACROINVERTEBRATE RESPONSES TO HABITAT HETEROGENEITY

INTRODUCTION

Southwood (1977) has suggested that the habitat acts as a templet on which the long-term survival strategies of organisms are developed and through which ill-adapted species are eliminated. Most studies of stream habitats have attempted to define the habitat in terms of the average conditions to which the organisms are exposed. However, correlations between the habitat components measured and the numbers (abundance) and kinds (taxonomic richness) of organisms have not provided a good statistical fit in most cases. Part of the lack of a good fit may be due to sampling deficiencies and improper selection of variables. But it also has become apparent that mean values may provide an inadequate characterization of the habitat (Southwood 1977, Minshall et al. 1988). Ecologists are beginning to recognize that stream habitats must be considered in terms of their variability (heterogeneity) in time and their heterogeneity in space (Horwitz 1970, Bruns et al. 1987). This belief results partly from the fact that in more constant (homogeneous) conditions, competition will be relatively intense and will limit the numbers and kinds of organisms, whereas more heterogeneous conditions will result in reduced competition and more complex communities (Connell 1978). Also, more heterogeneous environments are believed to provide a greater variety of living conditions and thus a greater ability to support more kinds of organisms than homogeneous ones (Pianka 1988).

The purpose of this study is to use bottom-dwelling macroscopic animals (benthic macroinvertebrates) to test the hypothesis that abundance (A)(as numbers and as biomass), richness (S), and diversity (some composite measure of A and S) in streams are primarily functions of habitat heterogeneity. The most important components of the habitat templet in streams are temperature, flow, substratum, and food (Minshall and Minshall 1977, Minshall 1984). Flow may be characterized in terms of volume (discharge) and velocity. Within a particular location (habitat) along a stream, temperature and discharge will vary little but change considerably with time. In contrast, velocity and substratum are mainly spatial variables and remain relatively constant over time. Food varies in amount both temporally and spatially but, in terms of a fixed sampling time, is mainly a spatial variable.

Many environmental factors are expected to vary in a predictable fashion along the length of river system (Vannote et al. 1980, Stanford and Ward 1983, Minshall et al. 1985a,b, Bruns et al. 1987). Thus it is reasonable to expect that distinct and predictable differences in the habitat templet will be associated the pattern of increasing stream size. Therefore, we chose to examine the role of habitat heterogeneity in determining the abundance and distribution of benthic macroinvertebrates, against a background of differences in stream size.

SITE DESCRIPTION

A difficulty with conducting a comparative study at several points along a relatively large river is that the impact of man may severely alter conditions and confound interpretation of the results. Therefore, we selected Big Creek, a relatively large, pristine river located in the Frank Church Wilderness of central Idaho as the focus of our study. Big Creek is one of the few large streams in Idaho still relatively unaffected by anthropogenic influences. A subsidiary reason for choosing this stream is that its ecology is unknown but is threatened by proposed mining activities in some parts of its headwaters (portions outside of the Wilderness).

Big Creek is classified as a 6th order stream according to the Strahler (1957) method of stream classification. According to this system, the smallest unbranched headwater tributary is designated as 1st order. The merging of two 1st order streams produces a 2nd order stream, two 2nd's a 3rd, etc. Big Creek and its tributaries were examined over stream orders two through 6 and at several different size locations within 6th order (Table 1). Link number (Shreve 1966), which gives a more precise measure of stream size than order, ranged from 10 at Cliff Creek to 912 in Big Creek above the gorge. Total link number for Big Creek is 938. Discharge, measured near base flow conditions, gave a ranking of the study streams similar to that of order and link (as expected) except that Beaver Creek, which had a lower stream order and link number than Ramey Creek, had almost twice the volume of flow. Slope ranged from 13% in 2nd order Cliff Creek to about 1% in the 5th and 6th order study reaches.

METHODS

Study sites were selected from examination of maps prior to entering the area, based on criteria of stream order and link and accessibility from the main Big Creek trail. An effort was made to choose locations of about the same elevation, to remove influences associated with this factor, but Ramey Creek and Beaver Creek deviated from this goal by roughly 200 and 400 m, respectively (Table 1). The number of sites was limited to one of each size by budgetary constraints and the exploratory nature of the study. All sites were sampled in August, prior to the Golden Fire which burned a number of drainages tributary to Big Creek in early September 1988. Each of the tributary streams studied was sampled several hundred meters upstream of its mouth.

Sampling methods utilized standard procedures which we have employed in other studies of Idaho streams (see e.g., Minshall 1981, 1986 and Minshall et al. 1982, 1983). The techniques and equipment have been developed specifically for use in remote back country areas over the past 10 years (Minshall et al. 1981 and unpublished, Bruns et al. 1987). However, several of the techniques used in this study were specifically developed or modified to permit measurement of habitat heterogeneity using indicators that can be assessed relatively quickly (i.e., without the need for continuous, long-term records).

Samples of benthic macroinvertebrates and associated organic matter were collected by means of a Surber net having a mesh of 250 um, preserved for transport to the laboratory, and processed as described by Platts et al. (1983). Invertebrates were identified to lowest taxonomic level practicable (usually genus), counted, and weighed to permit determination of richness, abundance (both numbers and biomass), and diversity. The associated plant matter was dried to a constant weight, burned in a muffle furnace at 500°C for

Table 1. Physical characterization of each study site.

Creek	Order	Link	Slope (%)	Elevation (m)	Discharge (m3/s)	Channel Width (m)	Channel Depth (m)	Water Width (m)
Cliff	2	10	13.0	1196.0	0.038	4.8	0.72	2.4
Beaver	3	26	4.0	1537.0	1.167	8.0	0.78	6.7
Ramey	4	47	3.5	1440.0	0.735	6.3	0.92	5.0
Rush	5	223	1.0	1171.0	1.614	15.1	1.20	9.3
Big/Coxey	6	414	1.5	1305.0	5.226	34.2	1.54	29.0
Big/Rush	6	627	1.5	1174.0	8.042	43.0	1.27	36.5
Big/Gorge	6	912	1.0	1122.0	8.834	43.2	1.30	32.1

3 h, and weighed to provide a measure of food abundance. Assessment of periphyton (attached algae) biomass and chlorophyll a content provided a second measure of food abundance (Robinson and Minshall 1986). Ten Surber and ten periphyton samples were collected from each site.

Temperature (°C) was measured with a maximum-minimum recording thermometer. The change in temperature between early morning low and mid-day high (Delta T_{daily}) gives a measure of relative variability in summer (Vannote et al. 1980, Vannote and Sweeney 1980). Since the August mid-day values were at or near the annual high and winter temperature values in the area are known to reach freezing, we also were able to estimate the annual Delta T. Summer-low discharge (~baseflow Q) was determined from measurements of stream width and mean cross-sectional water depth and velocity (0.6X depth) at the time of the study (August). Peak discharge was indexed by measuring the height above the streambed of stranded flotsam and by determining peak flow cross-sectional areas and avearage depth of peak flow. Relative temporal heterogeneity of discharge was determined as the ratio of depth (and x-sectional area) at baseflow to depth (and x-sectional area) at peak flow and as the difference of these measures between high and low flow conditions. Flow velocity was measured just above the substratum using a small Ott C-1 current meter at 50 random locations each within 100 m upstream and downstream of the discharge transect at each site. Substratum particle size was determined at the same locations by measuring the maximum, minimum, and intermediate axes of individual rocks (Leopold 1970). Spatial heterogeneity of depth, current velocity, and substratum particle size was assessed by calculation of coefficients of variation (Elliott 1977).

RESULTS and DISCUSSION

Habitat Heterogeneity and Stream Size

Substratum. No relationship of mean substrate size to stream size was evident from the data regardless of rock dimension used (Table 2). Mean substrate size, for each dimension measured, was not signifcantly different among stream sites as a consequence of large standard deviations. The variance/mean ratio gives an indication of the distribution pattern for a parameter of interest (Zar 1984). The variance/mean ratio for the substrate data was greater than 1 indicating a clumped or skewed distribution. The similarity in mean substrate size is evident in the similar coefficients of variation (CV's) among stream sites. CV's ranged from 75% to 93% for the x-axis, 61% to 90% for the y-axis, and 58% to 104% for the z-axis (Table 2b). In addition, the relatively high CV's indicate high substratum heterogeneity within all sites studied.

The similar results among substrate dimensions measured within and among stream sites tested indicate that a single dimension measurement is adequate to describe the substrate characteristics for a site. A correlation of the x-axis against either the y-axis (r=0.97) or z-axis (r=0.99) further supports this conclusion. (Figure 1). In addition, estimates of the sample size necessary, indicated that an N of 100 rocks was adequate at the 90% confidence level.

Table 2. Habitat characterization for the seven stream study sites. Values are expressed as means ± standard deviations and the coefficients of variation. Parameters measured include substratum, water depth, and water velocity.

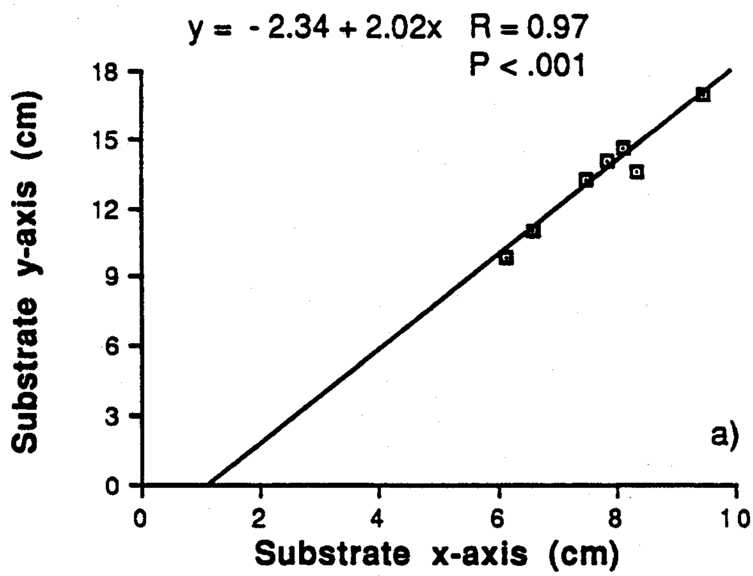
Mean±Standard deviation

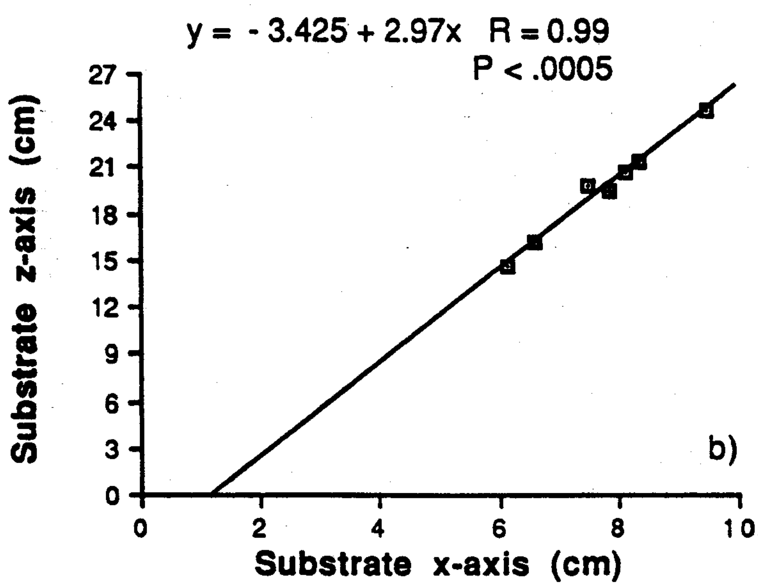
Creek	n	Substrate dimensions x-axis		y-axis		z-axis		Water depth (cm)		Velocity (m/s)	
Cliff	100	6.62	(5.07)	11.03	(6.74)	16.15	(10.22)	13.63	(7.21)	0.38	(0.29)
Beaver	100	7.49	(6.93)	13.22	(11.95)	19.89	(20.68)	26.10	(12.44)	0.45	(0.31)
Ramey	100	8.38	(6.29)	13.54	(9.25)	21.50	(16.10)	24.31	(12.32)	0.52	(0.40)
Rush	100	6.15	(5.09)	9.92	(8.50)	14.59	(14.03)	20.70	(8.73)	0.52	(0.35)
Big/Coxey	100	8.15	(6.10)	14.68	(9.50)	20.68	(11.98)	33.21	(15.34)	0.46	(0.30)
Big/Rush	100	9.48	(7.70)	16.97	(12.77)	24.66	(20.20)	36.14	(13.84)	0.45	(0.21)
Big/Gorge	100	7.89	(6.04)	14.02	(9.80)	19.50	(12.99)	42.90	(16.72)	0.44	(0.28)

Coefficient of Variation

Creek	n	Substrate dimensions x-axis	y-axis	z-axis	Water depth (cm)	Velocity (m/s)
Cliff	100	0.76	0.61	0.63	0.53	0.77
Beaver	100	0.93	0.90	1.04	0.48	0.68
Ramey	100	0.75	0.68	0.75	0.51	0.77
Rush	100	0.83	0.86	0.96	0.42	0.67
Big/Coxey	100	0.75	0.65	0.58	0.46	0.66
Big/Rush	100	0.81	0.75	0.82	0.38	0.46
Big/Gorge	100	0.77	0.70	0.67	0.39	0.64

Figure 1. Regressions of substrate x-axis to substrate y-axis (a) and to substrate z-axis (b). Points represent the mean axis length (N=100) for each site.


y = - 2.34 + 2.02x R = 0.97
P < .001
Substrate y-axis (cm)
Substrate x-axis (cm)
a)
0
3
6
9
12
15
18
0
2
4
6
8
10


y = - 3.425 + 2.97x R = 0.99
P < .0005
Substrate z-axis (cm)
Substrate x-axis (cm)
b)
0
3
6
9
12
15
18
21
24
27
0
2
4
6
8
10

estimates of the sample size necessary, indicated that an N of 100 rocks was adequate at the 90% confidence level.

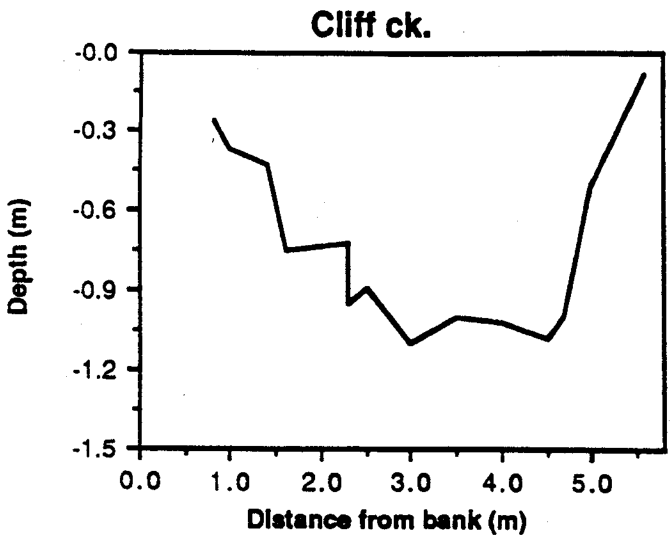
Water depth and channel characteristics. Mean water depth increased with stream size (number of links), ranging from a low of 13.6 cm for Cliff Creek (link number = 10) to 42.9 cm for Big Creek above the gorge (link number =912) (Table 2a). Coefficients of variation were relatively low for water depth ranging from 39 % to 53%, although CV's tended to decrease with stream size (Table 2b).

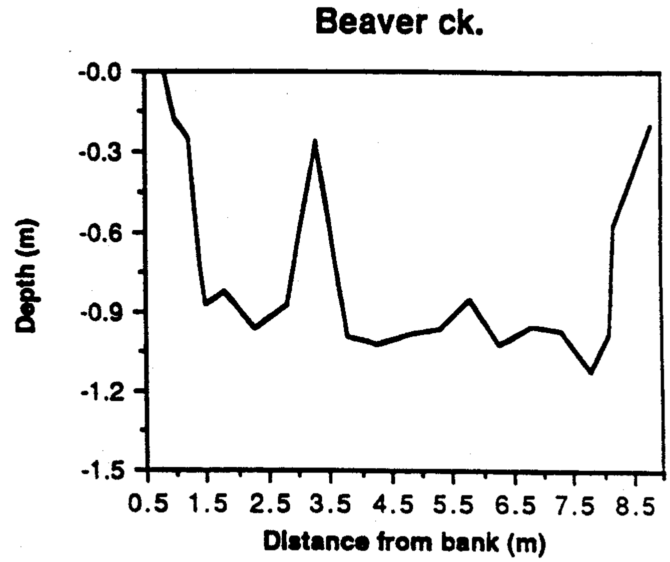
Channel width increased by 9X, while channel depth only increased 2X from Cliff Creek to Big Creek above the gorge (Table 1, Figure 2), and is evident in the positive correlation (r=0.89) of width/depth ratio to link number (Figure 3a). These data suggest that (1) streams tend to widen more than deepen in response to greater water flow (Leopold et al. 1964), or (2) the local geomorphology will dictate the degree of widening or deepening for a particular stream basin (Richards 1982). Observation of the Big Creek drainage suggests that this river tends to widen in the absence of strong geomorphic constraints, but many reaches showed significant limitation to the channel width imparted by narrowing of the canyon. Reaches used in this study showed an increase in width:depth ratio which would not have been as dramatic in other portions of the river, which attained low flow depths of greater than 2 m.

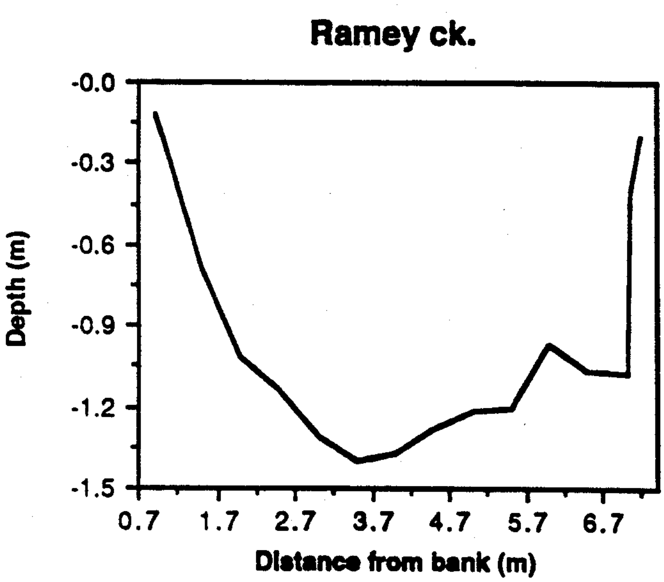
The ratios of baseflow water depth to bankfull water depth (D/D_b) and channel cross-sectional area at baseflow to bankfull cross-sectional area (A/A_b) provide an indication of temporal variation in flow within a stream site. The lower the ratio the greater the degree of change of water volume (Q) within a site. The ratio is low (i.e. close to 1) in smaller streams indicating that a high degree of change occurs in discharge due to runoff events. In contrast, peaks in discharge appear more pronounced in mid-sized streams due to local geomorphic influences on channel width (Leopold et al. 1964). Here, D/D_b should decrease relative to values found in 1st order streams. In large streams, increases in flow are not reflected by an increase in stream depth as as are increases in stream width; consequently, D/D_b should increase relative to values found in mid-sized streams. The data show relative increases in both ratio's in intermediate size streams (Figure 4; note: 1st order streams were not included in this study). Other indices of the relative temporal heterogeneity of discharge are the actual difference between baseflow depth and bankfull depth (Delta D) or channel area at baseflow and channel area at bankfull (Delta A) (Stanford and Ward 1983, Townsend 1989). Both indices showed positive relationships to link number, although Delta A provided a much better fit (r^2=0.96) than D/D_b, A/A_b, or Delta D (Figure 4).

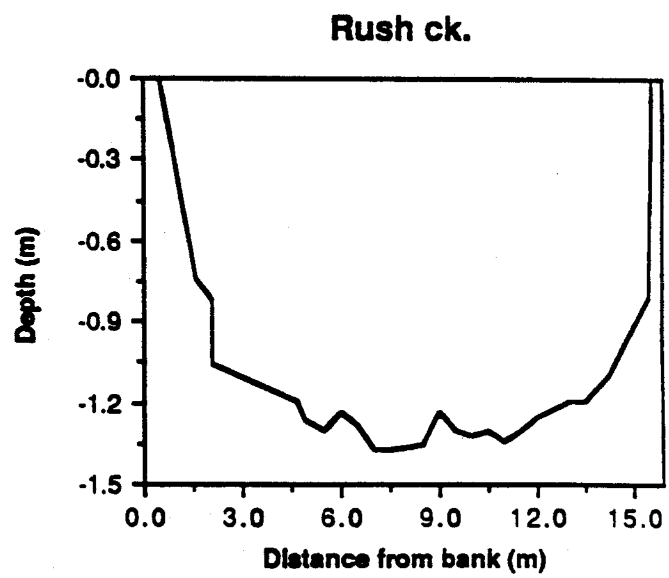
Water velocity. Mean water velocity was similar among sites and only ranged from 0.38 m/s at Cliff Creek to 0.52 m/s at Rush Creek (Table 2a). CV's also were similar among sites, ranging from 46% at Big Creek above Coxey Creek to 77% at Cliff Creek (Table 2b). These data indicate similar water velocity characteristics among sites. Slope had no apparent influence on water velocity (Figure 3b).

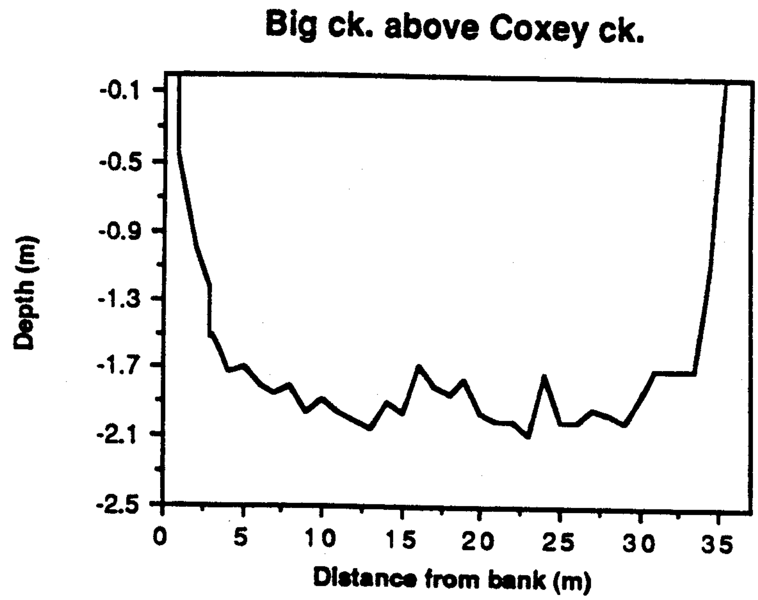
Figure 2. Cross-sectional channel profile for each site. Note changes in stream width compared to stream depth as stream size increases.

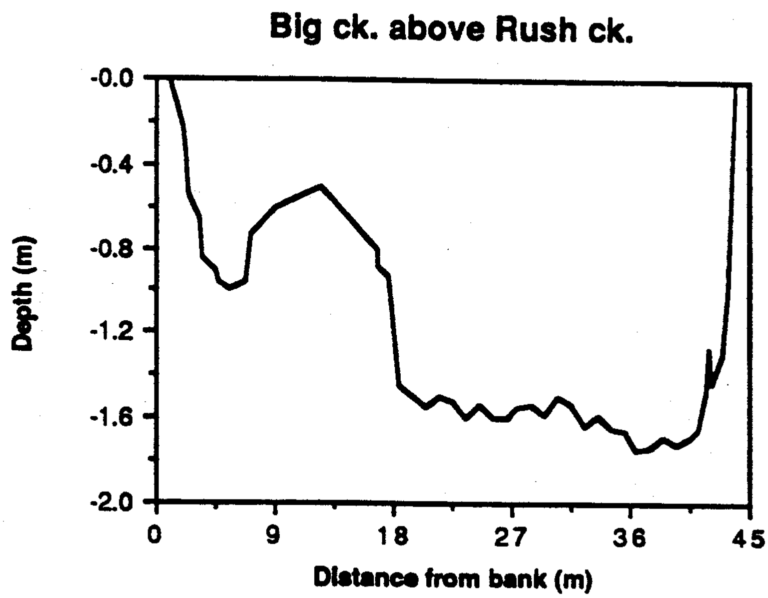

Cliff ck.
Depth (m)
-0.0
-0.3
-0.6
-0.9
-1.2
-1.5
0.0
1.0
2.0
3.0
4.0
5.0
Distance from bank (m)


Beaver ck.
Depth (m)
-0.0
-0.3
-0.6
-0.9
-1.2
-1.5
0.5
1.5
2.5
3.5
4.5
5.5
6.5
7.5
8.5
Distance from bank (m)


Ramey ck.
Depth (m)
-0.0
-0.3
-0.6
-0.9
-1.2
-1.5
0.7
1.7
2.7
3.7
4.7
5.7
6.7
Distance from bank (m)


Rush ck.
Depth (m)
-0.0
-0.3
-0.6
-0.9
-1.2
-1.5
0.0
3.0
6.0
9.0
12.0
15.0
Distance from bank (m)


Big ck. above Coxey ck.
Depth (m)
-0.1
-0.5
-0.9
-1.3
-1.7
-2.1
-2.5
0
5
10
15
20
25
30
35
Distance from bank (m)


Big ck. above Rush ck.
Depth (m)
-0.0
-0.4
-0.8
-1.2
-1.6
-2.0
0
9
18
27
36
45
Distance from bank (m)

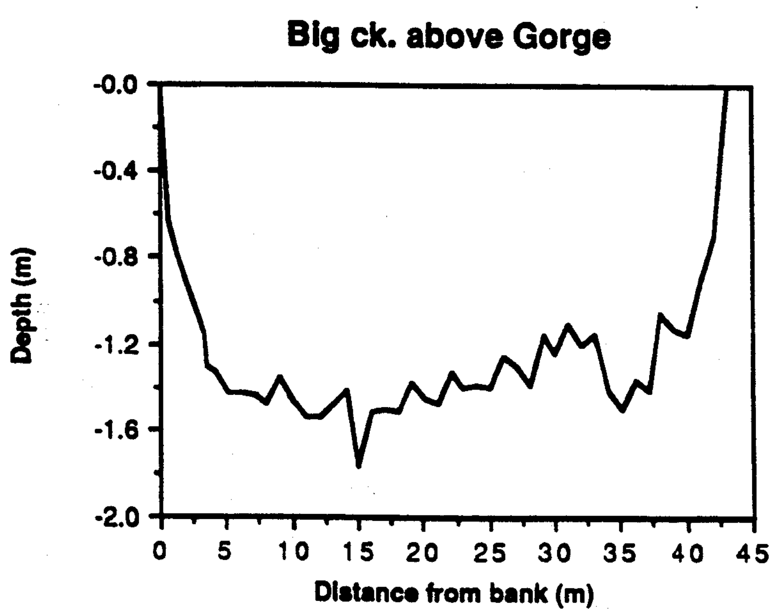
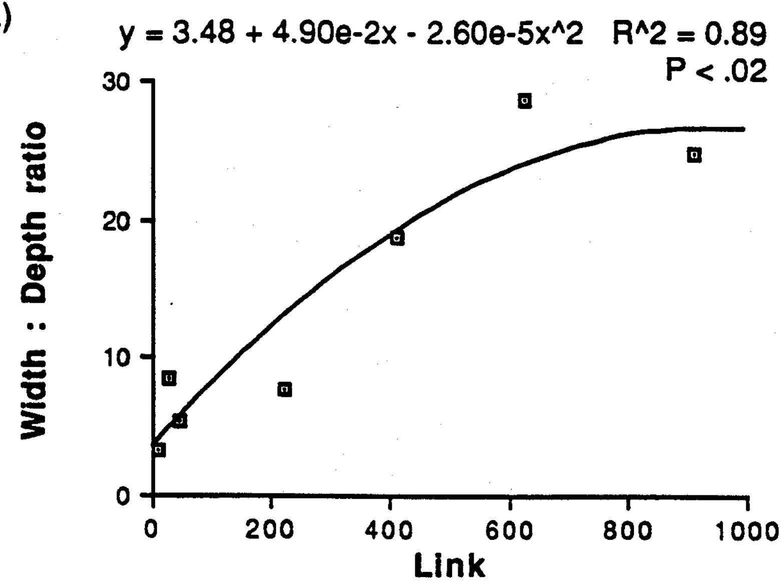

Big ck. above Gorge
Depth (m)
-0.0
-0.4
-0.8
-1.2
-1.6
-2.0
0
5
10
15
20
25
30
35
40
45
Distance from bank (m)

Figure 3. Regressions of stream link number against the width/depth ratio. Width and depth measurement derived from the cross-sectional profiles for each site. (b) Regression of channel slope (%) to mean current velocity. Mean velocity derived from 100 random points within each site.

a)


y = 3.48 + 4.90e-2x - 2.60e-5x^2 R^2 = 0.89
P < .02
Width : Depth ratio
Link
0
10
20
30
0
200
400
600
800
1000

b)

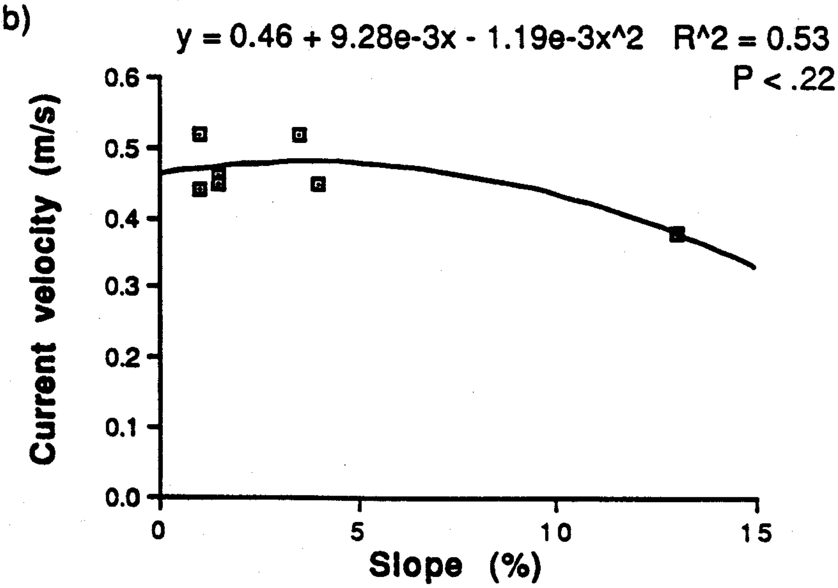
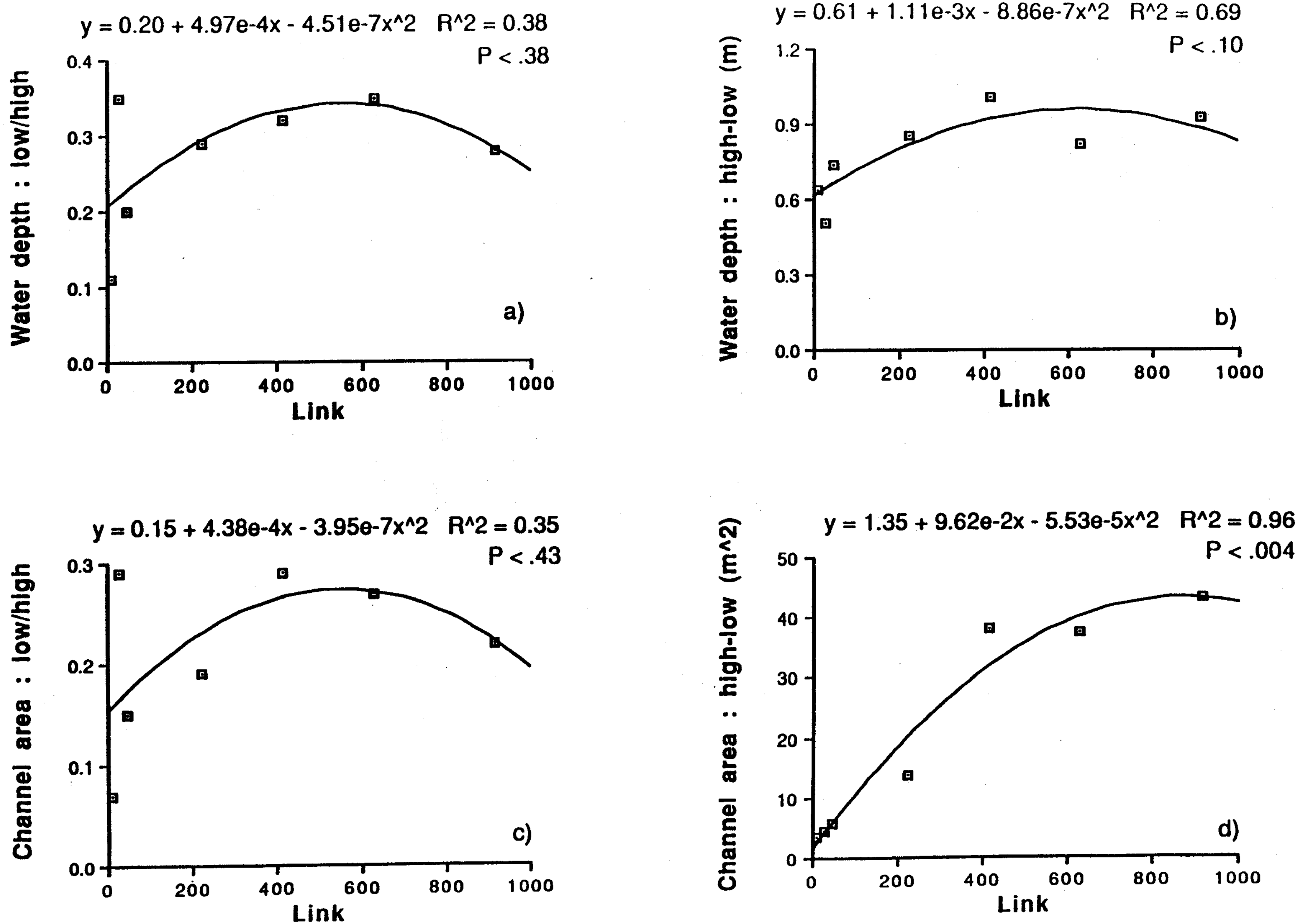

y = 0.46 + 9.28e-3x - 1.19e-3x^2 R^2 = 0.53
P < .22
Current velocity (m/s)
Slope (%)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0
5
10
15

Figure 4. Regressions of stream link number against (a) water depth ratio (D/D_b), (b) Delta-depth, (c) channel area ratio (A/A_b), and (d) Delta-area. Here, D=water depth at baseflow, D_b=water depth at bankfull, A=channel area at baseflow, A_b=channel area at bankfull, and Delta represents the difference between D to D_b, and A to A_b.


y = 0.20 + 4.97e-4x - 4.51e-7x^2   R^2 = 0.38
P < .38
Water depth : low/high
Link
a)
y = 0.61 + 1.11e-3x - 8.86e-7x^2   R^2 = 0.69
P < .10
Water depth : high-low (m)
Link
b)
y = 0.15 + 4.38e-4x - 3.95e-7x^2   R^2 = 0.35
P < .43
Channel area : low/high
Link
c)
y = 1.35 + 9.62e-2x - 5.53e-5x^2   R^2 = 0.96
P < .004
Channel area : high-low (m^2)
Link
d)

Temperature variation. Temporal variation in temperature was expressed in terms of the annual range in temperature and a near-maximum daily range in temperature. Both indices showed a strong positive relationship to stream size (daily Delta T, r=0.88; annual Delta T, r=0.90) (Figure 5a,b). Temporal variation in temperature is expected to be greatest in mid-sized streams and lowest in small and large size streams (Vannote et al. 1980, Vannote and Sweeney 1980). Our data fit this expected pattern as evidenced by the parabolic relationship in temperature variation for the Big Creek sites (Figure 5a,b).

Benthic and periphytic organic matter. The quantity of benthic organic matter (BOM) was high at Cliff Creek (98.38 g/m^2) and decreased as stream size increased (e.g. 5.0 g/m^2 at Big Creek above the gorge) (Table 3). Periphyton quantity was measured as chlorophyll a and ash-free-dry-mass (AFDM). Cliff Creek showed the lowest value of chlorophyll a at 0.24 ug/cm^2. An extremely large value was evident at Big Creek above the gorge giving this site a mean chlorophyll a level of 4.88 ug/cm^2. Deleting this value brought this site within the values found at the other sites (range 0.24 - 1.64 ug/cm^2)(Table 3). AFDM values were not significantly different among sites even though they ranged from 1.66 g/m^2 at Ramey Creek to 8.20 g/m^2 at Big Creek above Rush Creek (Table 3; with the single high value at Big Cr. above gorge removed) due to the high variation in values for Big Creek above Coxey and above Rush Creek.

Macroinvertebrate Response and Stream Size

Community level analyses. Rank-abundance curves provide a descriptive analysis of the relative distribution of taxa within a community and allow for comparisons among communities (Begon et al. 1986). All sites displayed similar rank-abundance curves with one taxon typically being predominant (Figure 6). The rank-abundance curves generally followed a log-normal distribution suggesting an intermediate level of community evenness.

Mean species richness (per sample) ranged from 38 taxa (at Ramey Creek) to 23.0 taxa (at Big Creek above Coxey Creek) (Figure 7a). Shannon-Weiner diversity (H') was higher in the smaller streams (H'=3.29) and tended to decrease in the larger streams (H'=2.62) (Figure 7b). Simpson's Dominance Index (C) was lower in the smaller streams (C=0.18, Cliff Creek) and higher in the larger streams (C=0.35, Big Creek above Coxey Creek) indicating a more even numerical distribution of taxa in the smaller streams and supporting inferences based on the H' values (Figure 7b). Mean numbers (#/m^2) and mean biomasses (mg/m^2) followed similar patterns. No obvious pattern was evident for abundance or biomass against stream size (Figure 7c,d).

Functional feeding group distribution and stream size. The River Continuum Concept (RCC) suggests expected patterns of functional feeding groups with stream size in relation to sources of energy inputs (Vannote et al. 1980). The energy base for the Big Creek drainage follows the typical model on which the RCC was based, thus patterns of functional feeding groups with stream size should adhere to the RCC predictions. According to these predictions, energy in headwater streams is primarily derived through allochthonous sources and thus shredders should be relatively more abundant. The relative abundances and biomasses of shredders was greater in the smaller headwater stream sites than the more open stream sites (Figure 8a, b). The benthic organic matter also was greater in these smaller streams.

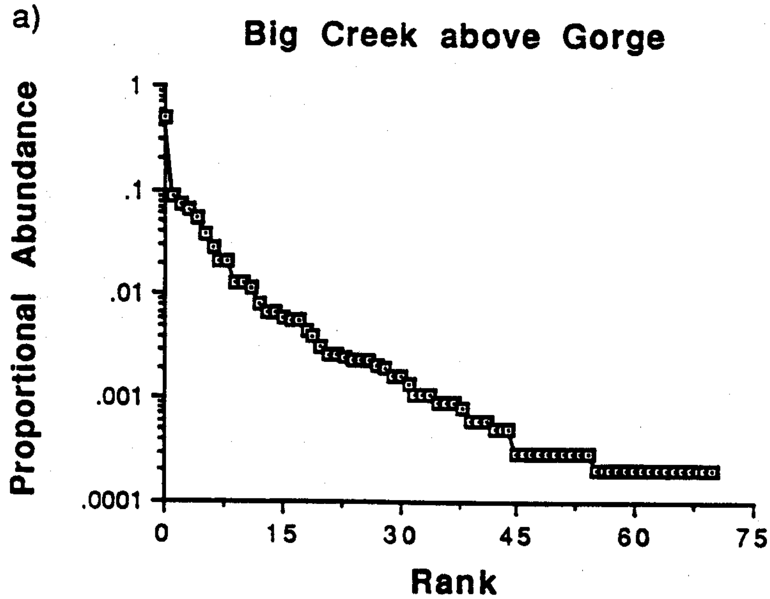
Figure 5. Regressions of stream link number to (a) daily Delta-temperature (^{o}C), and (b) annual Delta-temperature (^{o}C). Here, Delta-daily represents the difference between the maximum and minimum temperature recorded at the time of study, and Delta-annual represents the difference between the maximum temperature recorded at the time of study and minimum temperature of $0^{o}C$.

Table 3. Benthic organic matter (BOM), and periphyton levels as chlorophyll a and ash-free-dry-mass (AFDM). Values are expressed as means ± standard deviation.

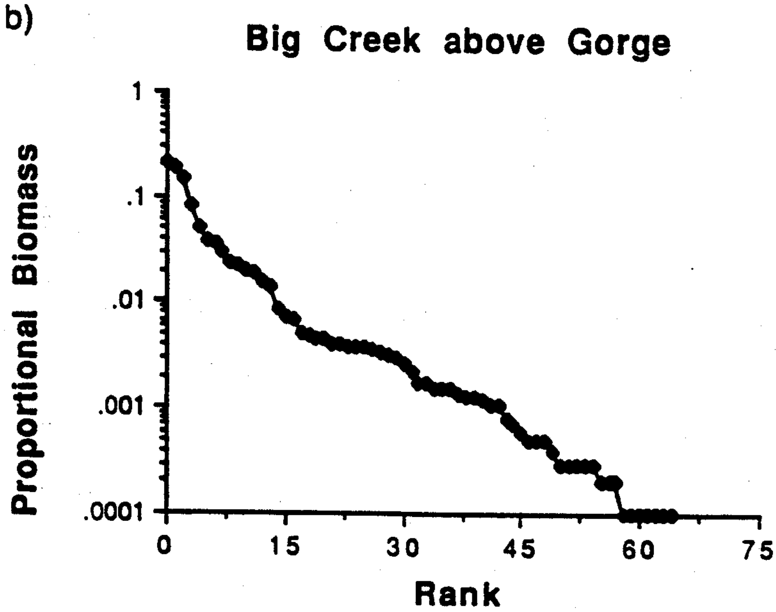
Station	n	BOM g/m2		Chlorophyll a µg/cm2		AFDM g/m2	
Cliff	10	98.38	(122.41)	0.24	(0.21)	1.93	(2.00)
Beaver	10	12.34	(21.89)	1.44	(2.38)	2.55	(2.93)
Ramey	10	12.11	(10.08)	0.94	(1.04)	1.66	(1.35)
Rush	10	18.41	(26.62)	0.65	(0.46)	2.49	(1.20)
Big/Coxey	10	19.53	(45.80)	1.64	(1.24)	7.28	(4.43)
Big/Rush	10	4.91	(4.03)	0.80	(0.63)	8.20	(7.32)
Big/Gorge	10	5.00	(3.17)	4.88	(12.33)	19.30	(52.32)
Big/Gorge *	9			0.99	(0.91)	2.76	(1.79)

* Values with outlier omitted.

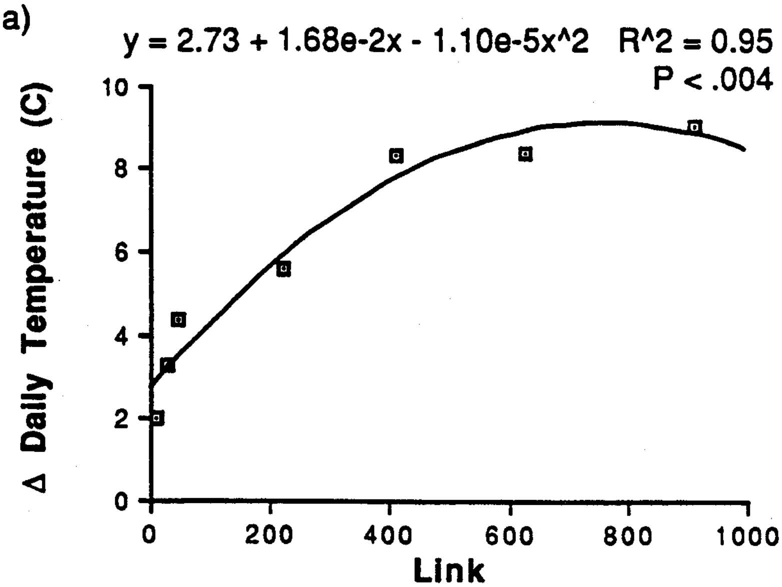
a)


Big Creek above Gorge
Proportional Abundance
1
.1
.01
.001
.0001
0
15
30
45
60
75
Rank

b)

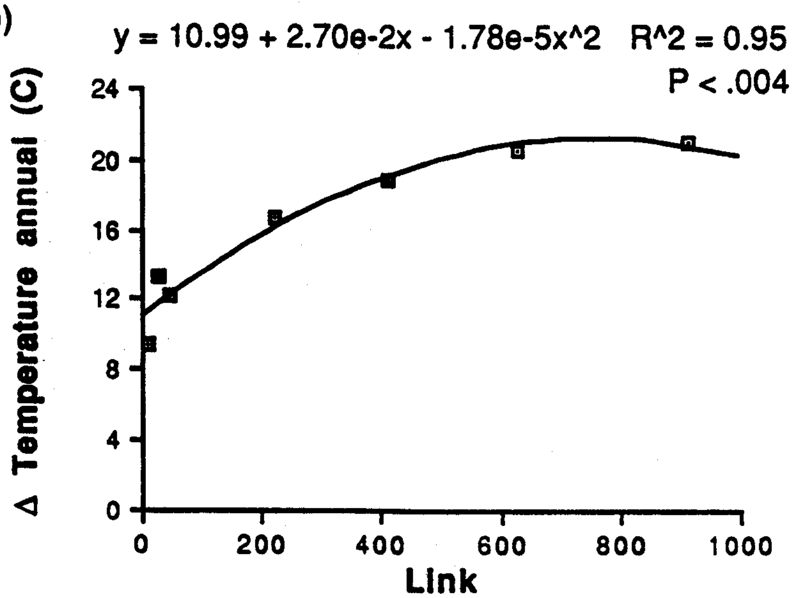

Big Creek above Gorge
Proportional Biomass
1
.1
.01
.001
.0001
0
15
30
45
60
75
Rank

a)



y = 2.73 + 1.68e-2x - 1.10e-5x^2   R^2 = 0.95
P < .004
Δ Daily Temperature (C)
0
2
4
6
8
10
0
200
400
600
800
1000
Link

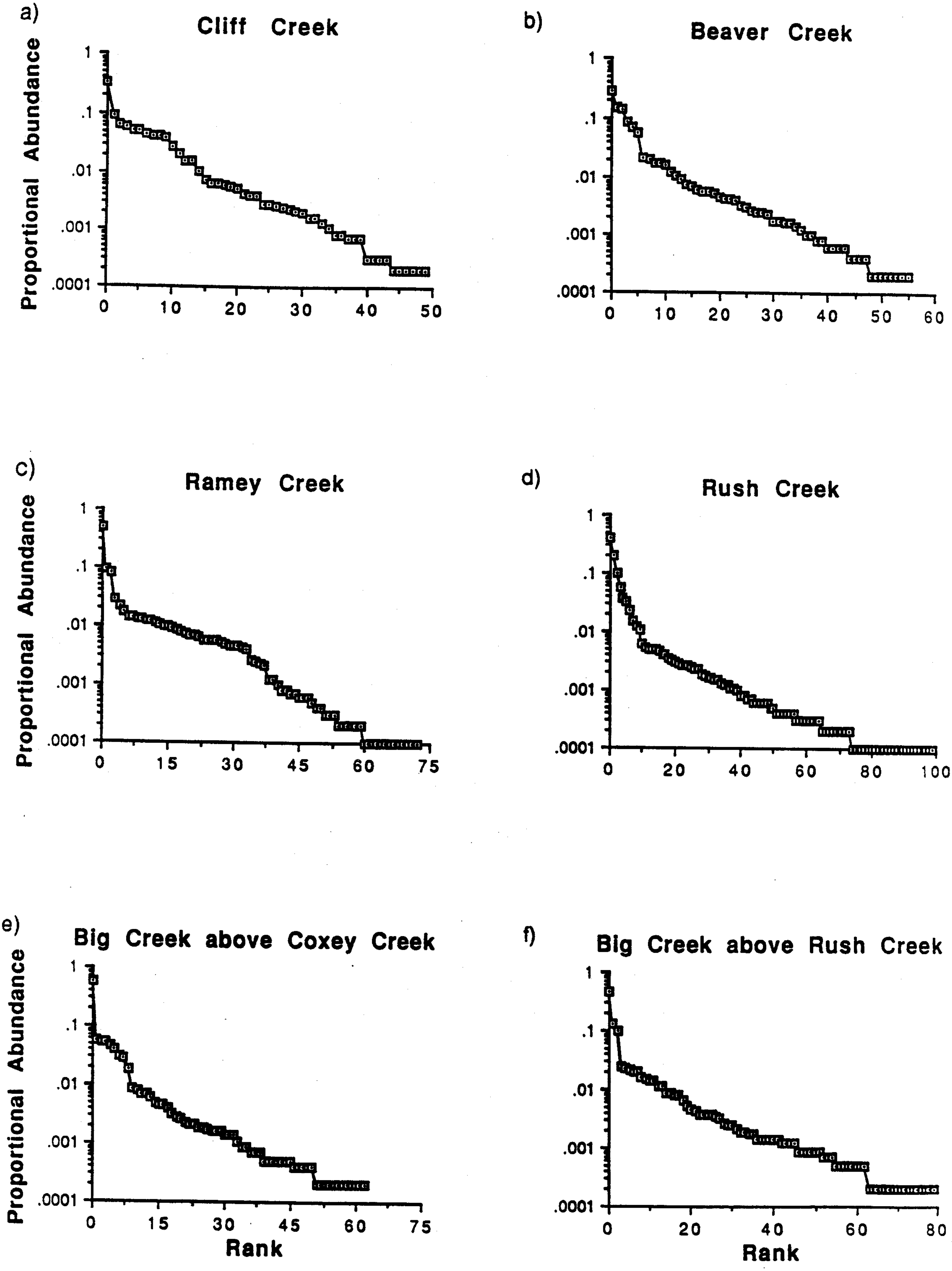
b)

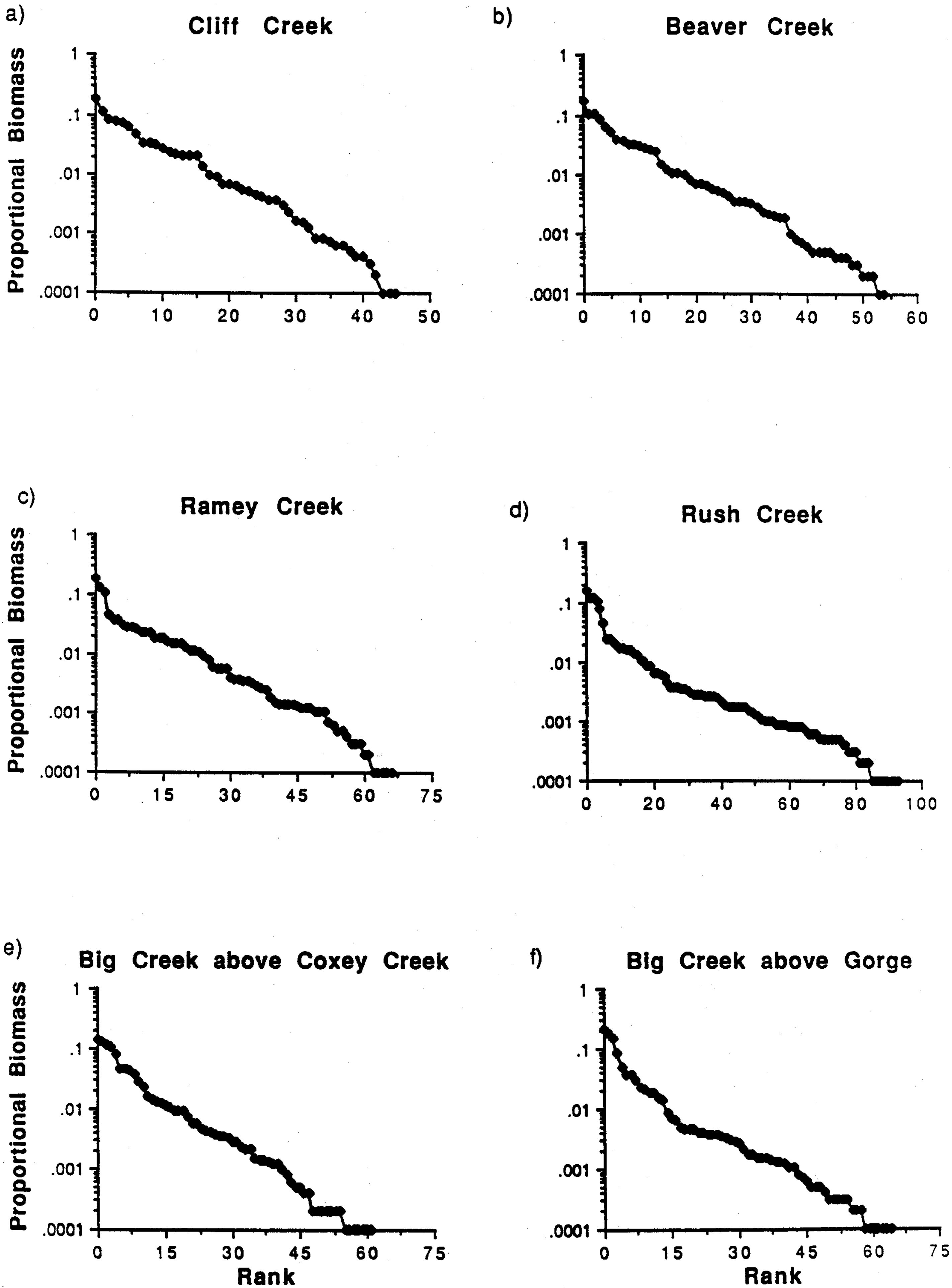


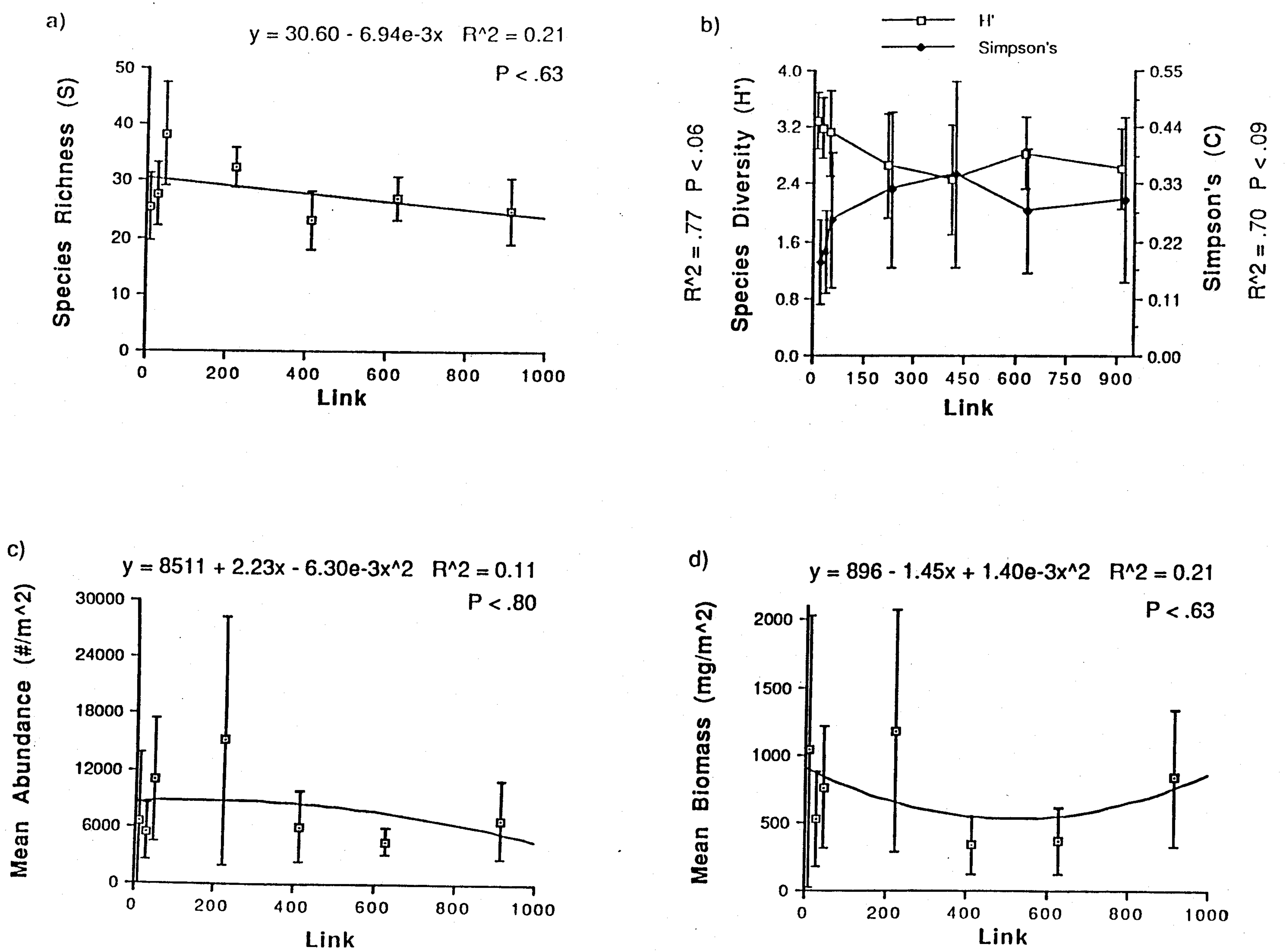
y = 10.99 + 2.70e-2x - 1.78e-5x^2   R^2 = 0.95
P < .004
Δ Temperature annual (C)
0
4
8
12
16
20
24
0
200
400
600
800
1000
Link

Figure 6. Proportional rank-abundance and rank-biomass curves for macroinvertebrates collected at each site. Note the similarity among curves and the log-normal distribution for each curve.

Figure 7. Regressions of stream link number against (a) mean species richness, (b) mean species diversity (H') and Simpson's dominance index (C), (c) mean total numbers ($\#/m^2$), and (d) mean biomass (mg/m^2). Each mean is derived from 10 benthic samples per site. N=7 for the regressions. Bars represent +1 SD.


a)
Cliff Creek
b)
Beaver Creek
c)
Ramey Creek
d)
Rush Creek
e)
Big Creek above Coxey Creek
f)
Big Creek above Rush Creek
Proportional Abundance
1
.1
.01
.001
.0001
Rank


a)
Cliff Creek
Proportional Biomass
1
.1
.01
.001
.0001
0
10
20
30
40
50
b)
Beaver Creek
1
.1
.01
.001
.0001
0
10
20
30
40
50
60
c)
Ramey Creek
Proportional Biomass
1
.1
.01
.001
.0001
0
15
30
45
60
75
d)
Rush Creek
1
.1
.01
.001
.0001
0
20
40
60
80
100
e)
Big Creek above Coxey Creek
Proportional Biomass
1
.1
.01
.001
.0001
0
15
30
45
60
75
Rank
f)
Big Creek above Gorge
1
.1
.01
.001
.0001
0
15
30
45
60
75
Rank



a)
y = 30.60 - 6.94e-3x R^2 = 0.21
P < .63
Species Richness (S)
0
10
20
30
40
50
0
200
400
600
800
1000
Link
b)
H'
Simpson's
R^2 = .77 P < .06
Species Diversity (H')
0.0
0.8
1.6
2.4
3.2
4.0
0
150
300
450
600
750
900
Link
0.00
0.11
0.22
0.33
0.44
0.55
Simpson's (C)
R^2 = .70 P < .09
c)
y = 8511 + 2.23x - 6.30e-3x^2 R^2 = 0.11
P < .80
Mean Abundance (#/m^2)
0
6000
12000
18000
24000
30000
0
200
400
600
800
1000
Link
d)
y = 896 - 1.45x + 1.40e-3x^2 R^2 = 0.21
P < .63
Mean Biomass (mg/m^2)
0
500
1000
1500
2000
0
200
400
600
800
1000
Link

Scrapers may or may not display obvious patterns with stream size depending upon the degree of canopy cover over the stream segment sampled (and therefore the amount of periphyton). The relative abundances of scrapers ranged from 10-27%, with no obvious pattern being exhibited (Figure 8c). This lack of pattern for scrapers is in agreement with the similarity in periphyton levels among sites. The relative biomass of scrapers ranged from 10% at Big/Coxey to nearly 40% at Big Creek above the gorge (Figure 8d). The low value for scrapers (and several other functional groups) at Rush Creek is associated with the predominance of filterers at this site (Figure 8e,f). Filterers were low in relative abundance (<10%) at all sites except Rush Creek (about 45%). The relative biomass of filterers appeared to be greater in the intermediate-sized stream sites (Figure 8f).

No obvious patterns were exhibited by the miner, gatherer, and predator functional groups in Big Creek (Figure 9a-e). These functional groups tend not to display patterns with stream size because relative amounts of BOM vary with local conditions, and the food base is not controlled autochthonously or allochthonously but is processed from either source. Also, these functional feeding groups generally are opportunistic . . . their abundances fluctuate in response to the sum total of foods available to them rather than to one particular food type. The biomass of predators at Big Creek above Rush Creek (Figure 9f) is unusually high. In addition, gatherers appeared to display high relative abundances and biomasses at Cliff Creek perhaps in response to the high level of benthic organic matter (98.4 g/m^2) found at this site (Figure 9c,d).

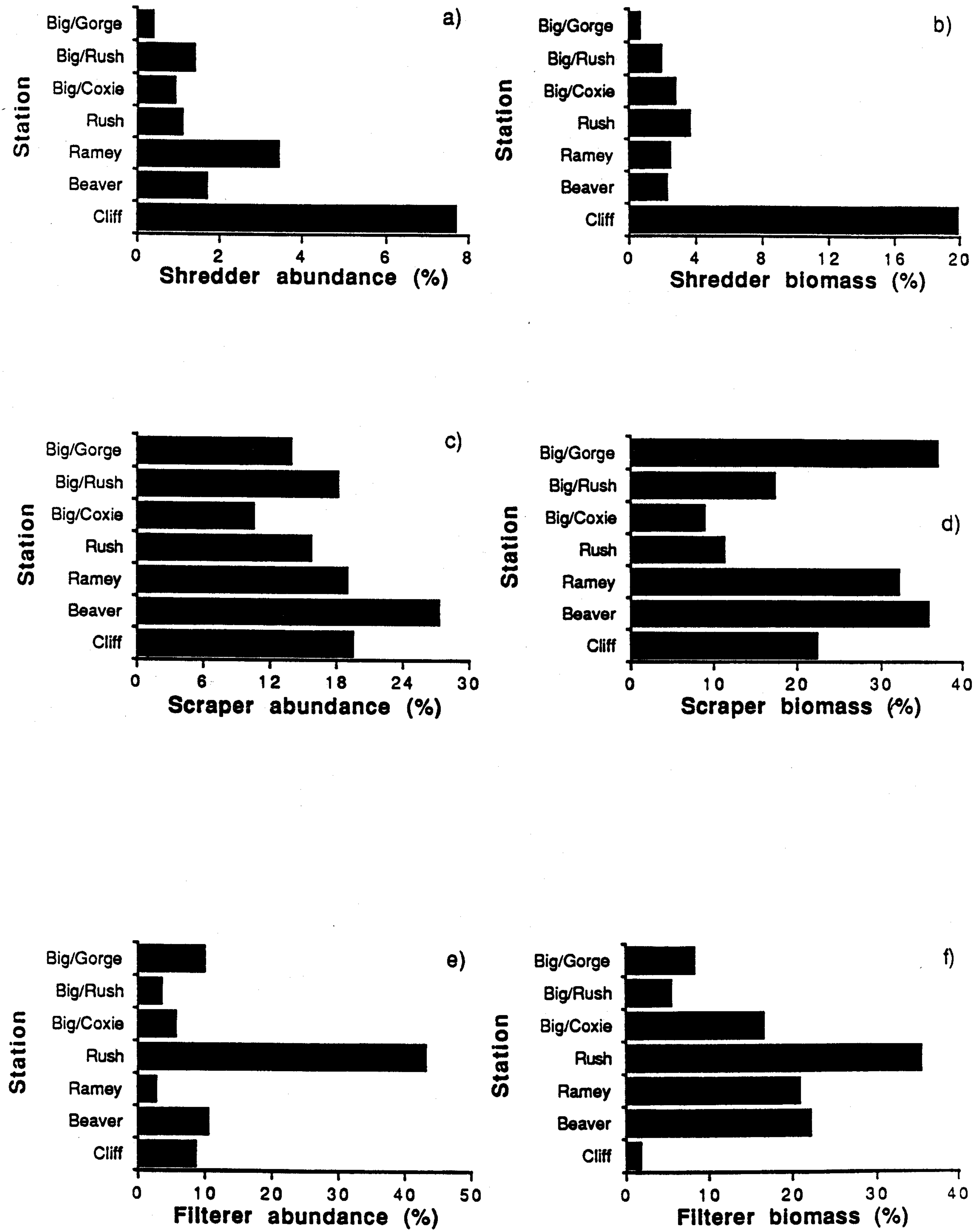
Macroinvertebrate taxon analyses. The top 10 macroinvertebrate taxa by total numbers and biomass were used in the analyses. The chironomids predominated at most sites (Table 4a). Simulium was the most abundant organism at Rush Creek, while tubificids were most abundant at Cliff and Ramey Creeks. The predominance of predators at Big Creek above Rush Creek was caused primarily by high numbers of Hydracarina (Table 4a).

The top 10 taxa by biomass for each site displayed different trends than the total numerical abundance data with large bodied organisms (e.g. large trichopterans and plecopterans) typically ranked number 1 (Table 4b). However, the chironomids still retained high ranking in respect to biomass. Brachycentrus and Simulium were ranked first and second at Rush Creek further emphasizing the predominance of filterers at this site. The Hydracarina dropped in rank at Big Creek above Rush Creek indicating the importance of body size for this parameter. Here, Hexatoma (a cranefly) was ranked first (Table 4b).

Macroinvertebrate Response to Habitat Characteristics

Community measures vs. habitat factors. Discussion in this section is oriented towards factors which proved to be significant to macroinvertebrate community structure. For measures of community structure, we used total numbers, total biomass, species richness (S), Shannon-Weiner diversity (H'), and Simpson's Index of diversity (C). As mentioned in the Introduction, certain environmental components within a given stream reach function primarily as spatial variables (e.g., substratum, depth, velocity, food) whereas others are chiefly temporal variables (e.g., changes in discharge and temperature). Of the four primary spatial measures we made (substratum particle size, water depth, current velocity, and food), velocity was the most consistently important in determining the structure of the macroinvertebrate

Figure 8. The mean relative abundance and biomass for the shredder, scraper, and filterer functional feeding groups by site. Each mean is based on 10 benthic samples.


a)
Station
Big/Gorge
Big/Rush
Big/Coxie
Rush
Ramey
Beaver
Cliff
0
2
4
6
8
Shredder abundance (%)
b)
Station
Big/Gorge
Big/Rush
Big/Coxie
Rush
Ramey
Beaver
Cliff
0
4
8
12
16
20
Shredder biomass (%)
c)
Station
Big/Gorge
Big/Rush
Big/Coxie
Rush
Ramey
Beaver
Cliff
0
6
12
18
24
30
Scraper abundance (%)
d)
Station
Big/Gorge
Big/Rush
Big/Coxie
Rush
Ramey
Beaver
Cliff
0
10
20
30
40
Scraper biomass (%)
e)
Station
Big/Gorge
Big/Rush
Big/Coxie
Rush
Ramey
Beaver
Cliff
0
10
20
30
40
50
Filterer abundance (%)
f)
Station
Big/Gorge
Big/Rush
Big/Coxie
Rush
Ramey
Beaver
Cliff
0
10
20
30
40
Filterer biomass (%)

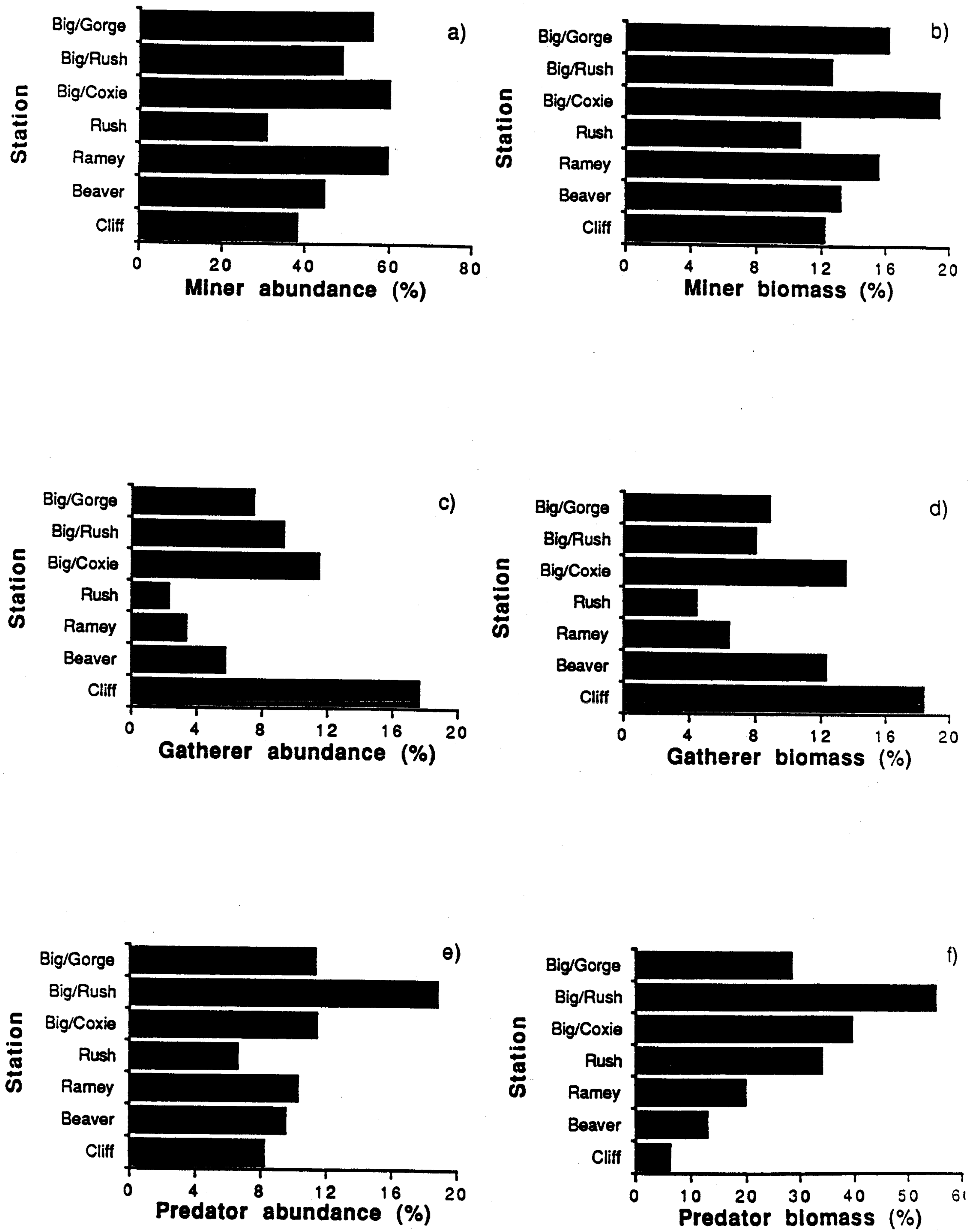

a)
Station
Big/Gorge
Big/Rush
Big/Coxie
Rush
Ramey
Beaver
Cliff
0
20
40
60
80
Miner abundance (%)
b)
Station
Big/Gorge
Big/Rush
Big/Coxie
Rush
Ramey
Beaver
Cliff
0
4
8
12
16
20
Miner biomass (%)
c)
Station
Big/Gorge
Big/Rush
Big/Coxie
Rush
Ramey
Beaver
Cliff
0
4
8
12
16
20
Gatherer abundance (%)
d)
Station
Big/Gorge
Big/Rush
Big/Coxie
Rush
Ramey
Beaver
Cliff
0
4
8
12
16
20
Gatherer biomass (%)
e)
Station
Big/Gorge
Big/Rush
Big/Coxie
Rush
Ramey
Beaver
Cliff
0
4
8
12
16
20
Predator abundance (%)
f)
Station
Big/Gorge
Big/Rush
Big/Coxie
Rush
Ramey
Beaver
Cliff
0
10
20
30
40
50
Predator biomass (%)

Figure 9. The mean relative abundance and biomass for the miner, gatherer, and predator functional feeding groups by site. Each mean is based on 10 benthic samples.

Table 4a. Mean abundance (#/m2) for the top ten taxa within each site.

Cliff Ck.	**#**	**Beaver Ck.**	**#**	**Ramey Ck.**	**#**	**Rush Ck.**	**#**
Tubificidae	198.4	Chironomidae	144.0	Tubificidae	515.7	Simulium sp.	568.2
Cinygmula sp.	57.9	Tubificidae	79.5	B. tricaudatus	97.6	Chironomidae	284.5
Polycentropus sp.	40.7	Baetis parvus	71.0	Chironomidae	30.4	Tubificidae	143.0
Heterlimnius sp.	36.3	Simulium sp.	43.9	Ephemerella inermis	22.4	B. bicaudatus	83.0
Chironomidae	33.1	Epeorus longimanus	36.4	Rhyacophila angelita	17.5	Hydracarina	54.4
Alloperla sp.	32.4	Cinygmula sp.	28.4	Perlidae	14.5	B. tricaudatus	46.1
Baetis parvus	29.3	Plecoptera	10.8	Chironomidae pupae	14.5	Hydroptila sp.	33.2
Simulium sp.	26.7	Polycentropus sp.	10.6	Heterlimnius sp.	13.9	B. intermedius	22.3
Nematoda	25.8	Hydracarina	9.0	Parapsyche sp.	13.8	Brachycentrus sp.	18.0
Ostracoda	25.6	Cultus sp.	8.7	Epeorus deceptivus	13.1	Cinygmula sp.	15.6
Big/Coxey	**#**	**Big/Rush**	**#**	**Big/Gorge**	**#**		
Chironomidae	322.0	Chironomidae	196.0	Chironomidae	304.2		
Lepidostoma sp.	32.8	Hydracarina	54.2	Hydracarina	55.1		
B. tricaudatus	29.9	B. tricaudatus	40.9	Tubificidae	47.6		
Hydracarina	29.4	Attenella sp.	10.3	B. tricaudatus	41.3		
Brachycentrus sp.	26.1	Lepidostoma sp.	9.6	Simulium sp.	35.0		
Cinygmula sp.	22.6	Chironomidae pupae	8.9	Lymnaea	24.6		
Hydrovatus sp.	17.3	Optioservus sp.	8.4	Optioservus sp.	18.2		
Tubificidae	15.9	Hydropsyche sp.	8.3	Lepidostoma sp.	13.7		
Trichoptera "B"	10.2	Nematoda	6.7	Hydropsychidae	13.5		
Trichoptera "C"	4.9	Ephemerella aurivilli	6.6	Physidae	8.3		

Table 4b. Mean biomass (mg/m2) for the top ten taxa within each site.

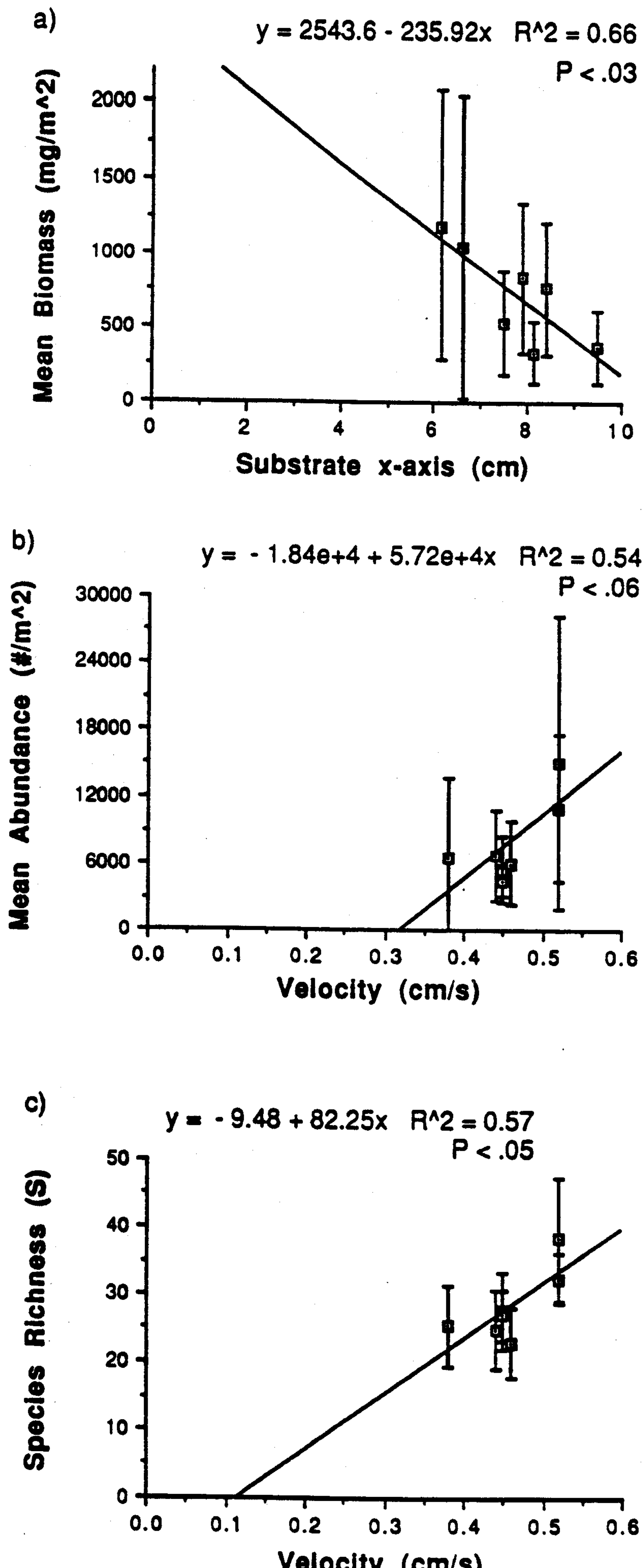
Cliff Ck.	mg	Beaver Ck.	mg	Ramey Ck.	mg	Rush Ck.	mg
Tipula sp.	11.17	Arctopsyche grandis	8.72	Parapsyche elis	13.73	Brachycentrus sp.	18.05
Drunella colordensis	8.50	Epeorus longimanus	5.50	Tubificidae	9.48	Simulium sp.	14.04
Cinygmula sp.	8.08	Baetis parvus	5.33	B. tricaudatus	7.62	Hesperoperla pacifica	13.53
Lumbriculus sp.	6.22	Chironomidae	4.29	Drunella colordensis	3.39	Atherix variagata	11.64
Tubificidae	4.74	Cinygmula sp.	3.18	Rhyacophila vaccua	2.72	Chironomidae	8.67
Heterlimnius sp.	3.41	Drunella spinifera	2.69	Cinygmula sp.	2.61	Hexatoma sp.	4.97
Rhyacophila acropedes	3.29	Tubificidae	2.04	Epeorus longimanus	2.06	Tubificidae	2.76
Polycentropus sp.	3.17	Turbellaria	1.92	Glutops sp.	1.99	Hydropsyche sp.	2.69
Ampumixis sp.	2.70	Trichoptera pupae	1.68	Drunella doddsi	1.95	Limnephilus sp.	2.38
Baetis parvus	2.42	Serratella tibialis	1.65	Turbellaria	1.67	Hydroptila sp.	2.01
Big/Coxey	**mg**	**Big/Rush**	**mg**	**Big/Gorge**	**mg**		
Chironomidae	4.45	Hexatoma sp.	11.17	Lymnaea	16.35		
Hesperoperla pacifica	4.18	Chironomidae	3.99	Hexatoma sp.	14.67		
Brachycentrus sp.	3.48	Classenia sp.	2.85	Chironomidae	11.73		
Hexatoma sp.	3.38	B. tricaudatus	1.96	Physidae	6.56		
Lepidostoma sp.	2.49	Attenella sp.	1.31	Hydropsyche sp.	3.95		
Arctopsyche grandis	1.48	Hydropsyche sp.	1.22	B. tricaudatus	2.90		
Atherix variagata	1.43	Hydracarina	1.07	Attenella sp.	2.88		
B. tricaudatus	1.36	Ephemerella aurivilli	1.02	Classenia sp.	2.37		
Lumbriculus sp.	1.15	Hesperoperla pacifica	0.99	Epeorus longimanus	1.80		
Hydracarina	0.89	Atherix variagata	0.84	Hydracarina	1.74		

assemblage among sites. Velocity coefficients of determination (r^2 values) of regressions were > 0.50 against three of the five community indicies measured (Table 5, Figure 10b-d). Substratum size (x-axis) displayed a higher r^2 value, showing a significant negative relationship against mean biomass of invertebrates (Figure 10a). Rabeni and Minshall (1977) found the greatest numbers of invertebrates on 2.5 - 3.5 cm diameter substratum sizes and markedly fewer on >7 and <2 cm diameter particle sizes. Their findings support the negative linear relationship shown in Figure 10a but suggest that it probably would become curvilinear below 1 - 2 cm diameter, wherever such deposits are found in the Big Creek basin. There were no strong relationships indicated by depth or the CV of depth. Statistically significant positive regressions were found for velocity against mean numbers and species richness (Figure 10b,c). Several trends were evident in regressions of food parameters against macro-invertebrate parameters (Table 5). Mean biomass showed a negative relationship against both AFDM and chlorophyll a (Figure 14a,b). Mean H' displayed a hyperbolic pattern when regressed against AFDM (Figure 14c). The highest, and only significant correlations, were for H'($p > 0.02$) and C ($p >0.01$) against spatial heterogeneity of periphyton biomass. Greater insight into the influence of food on macroinvertebrates is provided at a finer resolution of analysis (e.g. functional feeding groups, or taxon-specific analysis).

Collectively, the temporal variables accounted for more and stronger correlations when regressed against community measures than did the spatial variables (Table 5). Four measures of discharge heterogeneity were evaluated in this study: (1) channel cross-sectional area at low discharge (A) to that at bankfull discharge (A_b), (2) water depth at low discharge (D) to that at bankfull discharge (D_b), (3) annual change in channel cross-sectional area (Delta A), and (4) annual change in water depth (Delta D). Mean biomass of macroinvertebrates expressed a significant negative regression against A/A_b (Figure 11a). Mean numbers of invertebrates displayed strong but nonsignificant parabolic relationships against A/A_b and D/D_b (Figure 11b,c). Simpson's index also tended to peak at intermediate levels of D/D_b (Figure 11d). Shannon-Wiener diversity (H') values were intermediate at intermediate levels of Delta A but showed a negative relationship with Delta D (Figure 12a,b), whereas Simpson's dominance index showed a parabolic pattern against Delta A and a linear increase with Delta D (Figure 12c,d). These data indicate a less even distribution of taxa at intermediate levels of habitat variation as determined through D/D_b and Delta A. In contrast, the macroinvertebrate assemblages are dominated by progressively fewer taxa as Delta D increased. Overall, A/A_b gave the best fit for biomass (linear) and numbers (parabolic) and Delta D the best fit for H' and C. There was no apparent or significant relationship between these measures of discharge variability and species richness.

Variation in temperature, expressed daily or annually, also plays an important role in the structure of macroinvertebrate assemblages (Stanford and Ward 1983). Simpson's index displayed strong parabolic regressions against both Delta T-annual, and Delta T-daily, suggesting that at even greater variations in temperature this parameter should decrease further (Figure 13a,b). Shannon-Wiener diversity displayed strong negative regressions against both Delta T-annual and Delta T-daily (Figure 13c,d) instead of a hyperbolic pattern, which would have corroborated the trend shown by Simpson's index. Mean numbers and species richness (S) displayed parabolic patterns against Delta T-daily (Figure 13e,f). These data support our earlier findings for the main Salmon River that species richness is highest and the distribution of taxa within macroinvertebrate assemblages less even at some intermediate level

Figure 10. Regressions of (a) mean substrate x-axis (cm) against mean biomass (mg/m^2) of macroinvertebrates, (b) mean velocity (cm/s) against mean abundance ($\#/m^2$), (c) mean velocity (cm/s) against species richness (S), and (d) the coefficient of variation of velocity against species diversity (H'). For each mean N=10, and n=7 for each regression. Bars represent +1 SD.



a)
y = 2543.6 - 235.92x R^2 = 0.66
P < .03
Mean Biomass (mg/m^2)
0
500
1000
1500
2000
0
2
4
6
8
10
Substrate x-axis (cm)
b)
y = - 1.84e+4 + 5.72e+4x R^2 = 0.54
P < .06
Mean Abundance (#/m^2)
0
6000
12000
18000
24000
30000
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Velocity (cm/s)
c)
y = - 9.48 + 82.25x R^2 = 0.57
P < .05
Species Richness (S)
0
10
20
30
40
50
0.0
0.1
0.2
0.3
0.4
0.5
0.6

Figure 11. Regressions of channel area ratio (A/A_b) to (a) mean biomass (mg/m^2) and (b) mean abundance ($\#/m^2$); and of water depth ratio (D/D_b) against (c) mean abundance and (d) Simpson's dominance index (C). Ratios determined as in Figure 4. Sample size as in Figure 10. Bars represent +1 SD.

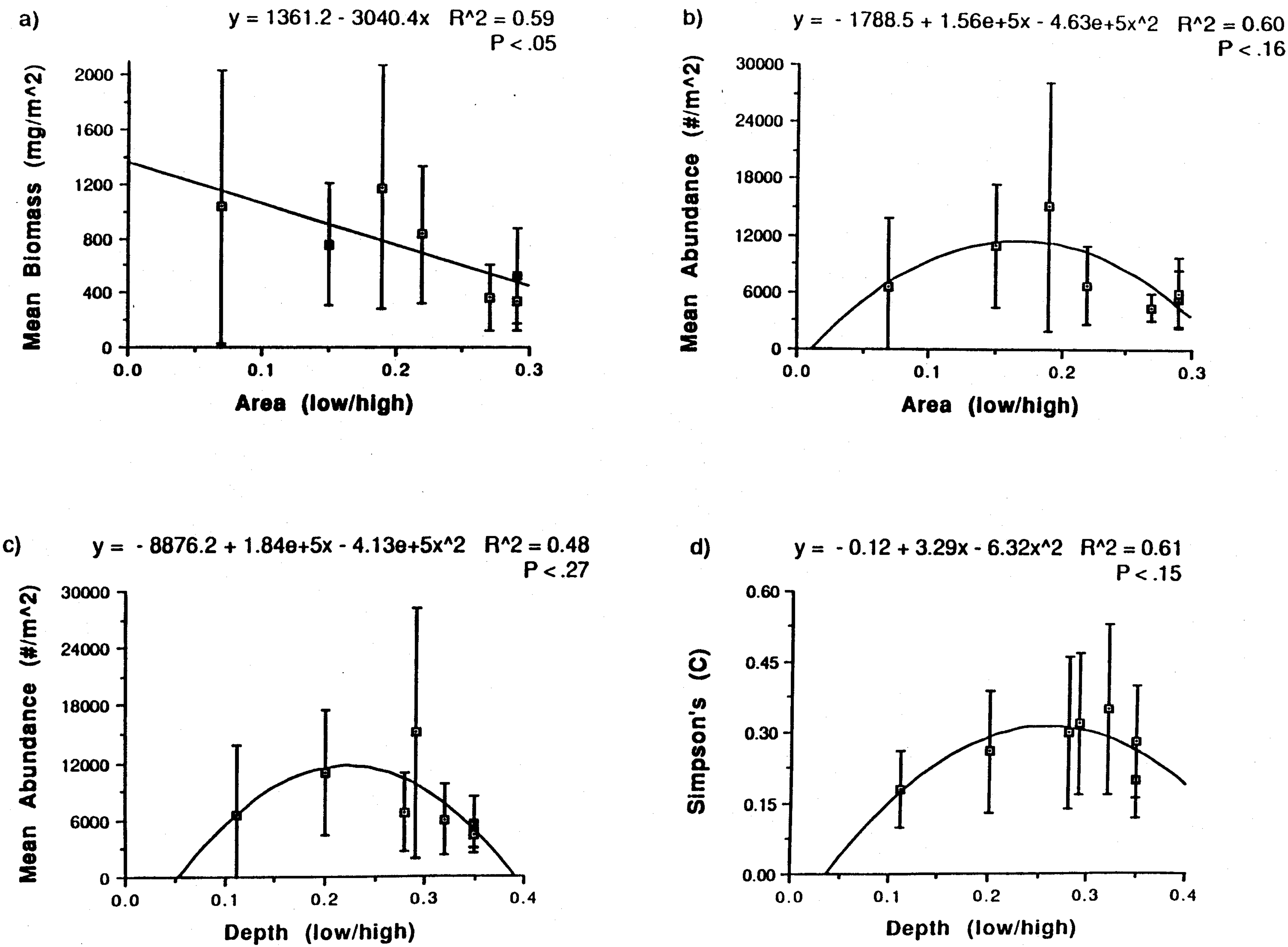
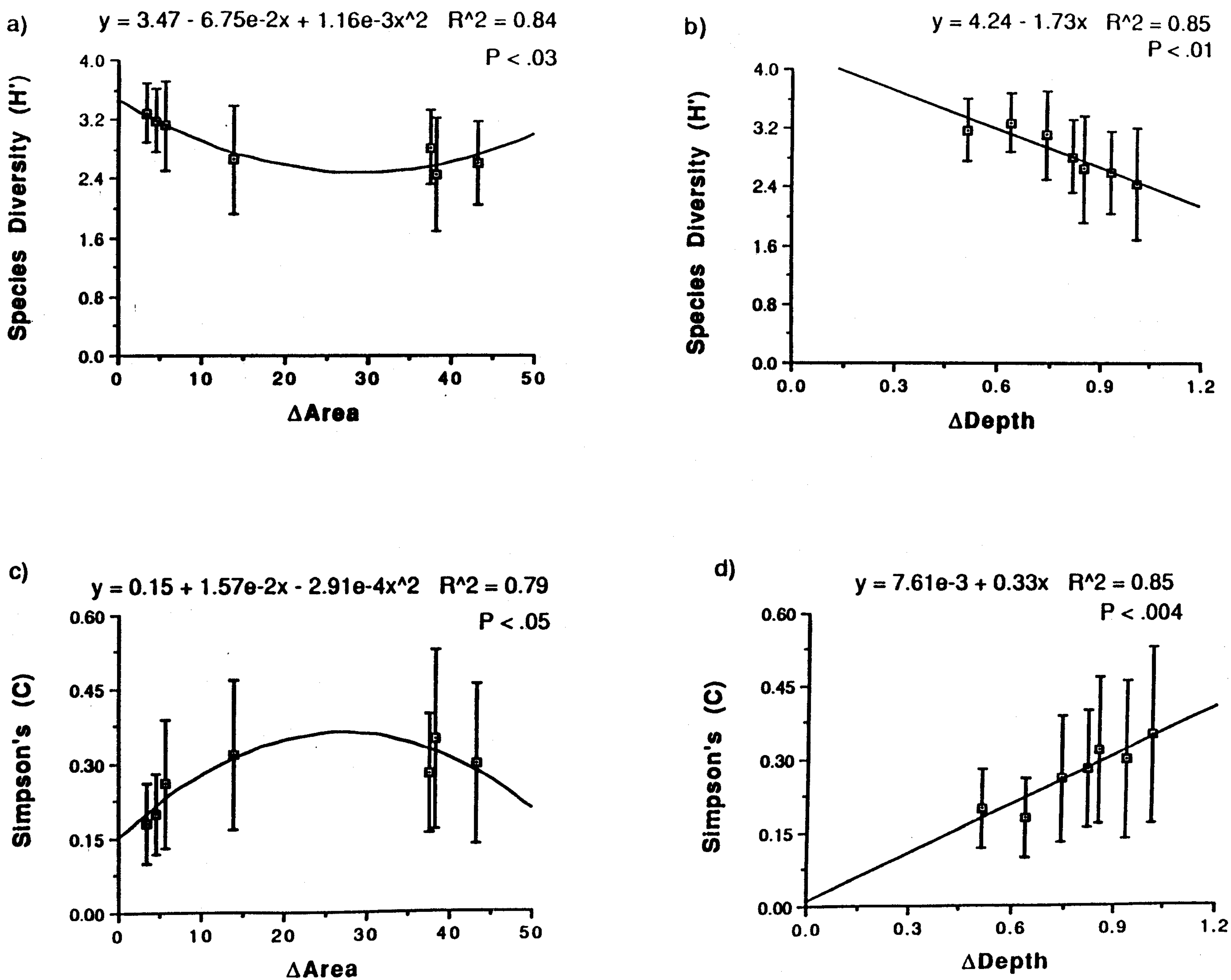
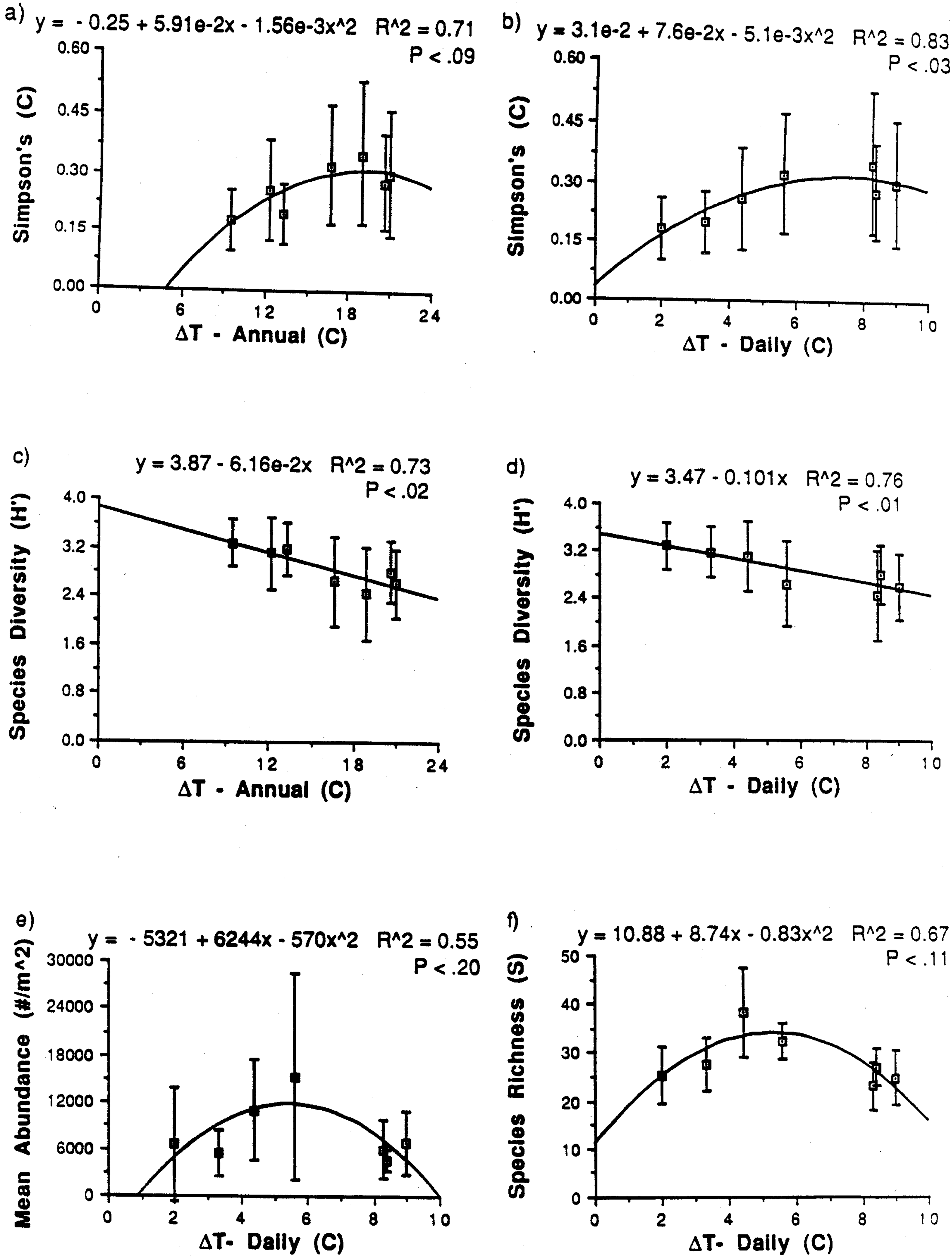

a)
y = 1361.2 - 3040.4x R^2 = 0.59
P < .05
Mean Biomass (mg/m^2)
2000
1600
1200
800
400
0
0.0
0.1
0.2
0.3
Area (low/high)
b)
y = - 1788.5 + 1.56e+5x - 4.63e+5x^2 R^2 = 0.60
P < .16
Mean Abundance (#/m^2)
30000
24000
18000
12000
6000
0
0.0
0.1
0.2
0.3
Area (low/high)
c)
y = - 8876.2 + 1.84e+5x - 4.13e+5x^2 R^2 = 0.48
P < .27
Mean Abundance (#/m^2)
30000
24000
18000
12000
6000
0
0.0
0.1
0.2
0.3
0.4
Depth (low/high)
d)
y = - 0.12 + 3.29x - 6.32x^2 R^2 = 0.61
P < .15
Simpson's (C)
0.60
0.45
0.30
0.15
0.00
0.0
0.1
0.2
0.3
0.4
Depth (low/high)

Figure 12. Regressions of (a) Delta-area to species diversity (H'), (b) Delta-depth to species diversity (H'), (c) Delta-area to Simpson's index (C), and (d) Delta-depth to Simpson's index (C). Sample size as in Figure 10. Bars represent +1 SD.



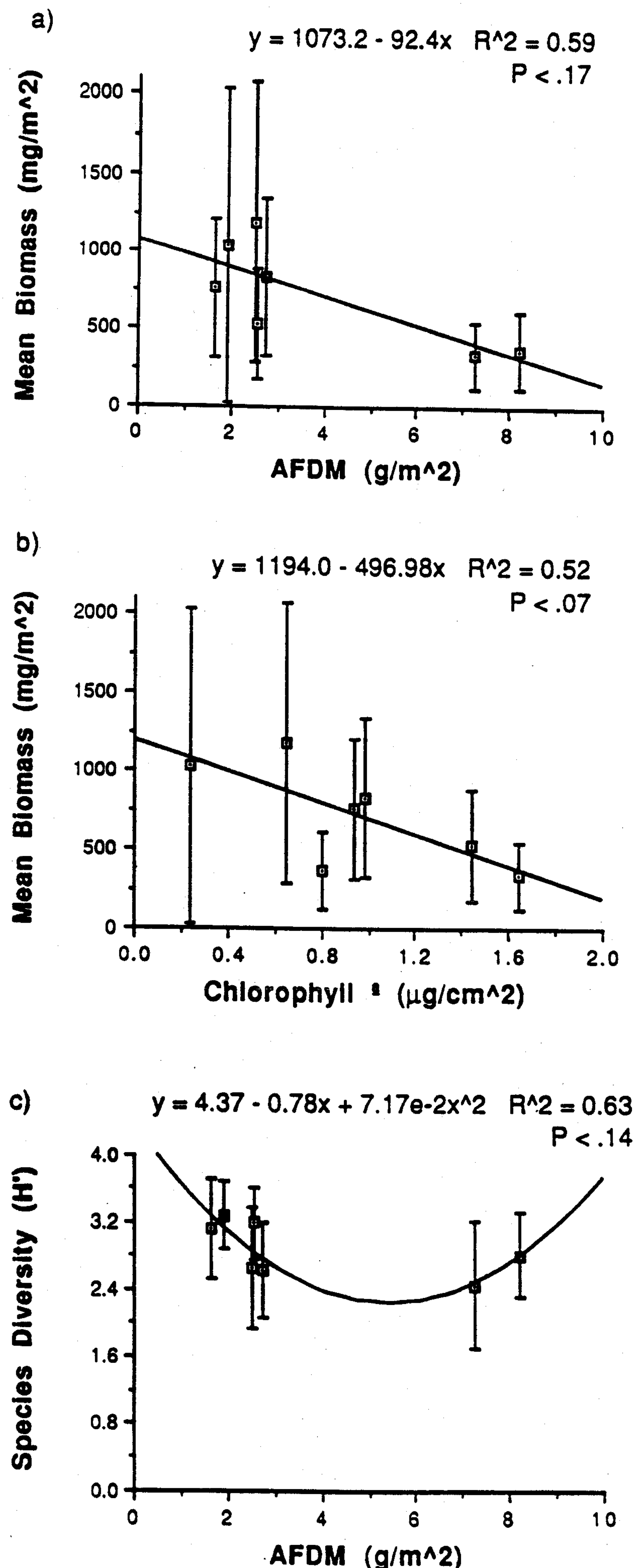
a)
y = 3.47 - 6.75e-2x + 1.16e-3x^2   R^2 = 0.84
P < .03
Species Diversity (H')
4.0
3.2
2.4
1.6
0.8
0.0
0
10
20
30
40
50
ΔArea
b)
y = 4.24 - 1.73x   R^2 = 0.85
P < .01
Species Diversity (H')
4.0
3.2
2.4
1.6
0.8
0.0
0.0
0.3
0.6
0.9
1.2
ΔDepth
c)
y = 0.15 + 1.57e-2x - 2.91e-4x^2   R^2 = 0.79
P < .05
Simpson's (C)
0.60
0.45
0.30
0.15
0.00
0
10
20
30
40
50
ΔArea
d)
y = 7.61e-3 + 0.33x   R^2 = 0.85
P < .004
Simpson's (C)
0.60
0.45
0.30
0.15
0.00
0.0
0.3
0.6
0.9
1.2
ΔDepth

Figure 13. Regressions of (a) annual Delta-T against Simpson's index (C), (b) daily Delta-t against Simpson's index (C), (c) annual Delta-T against species diversity (H'), and daily Delta_T against (d) species diversity(H'), (e) mean abundance (#/m^2), and (f) species richness (S). Delta-T as in Figure 5. Sample size as in Figure 10. Bars represent +1 SD.



a) y = - 0.25 + 5.91e-2x - 1.56e-3x^2 R^2 = 0.71
P < .09
Simpson's (C)
0.60
0.45
0.30
0.15
0.00
0 6 12 18 24
ΔT - Annual (C)
b) y = 3.1e-2 + 7.6e-2x - 5.1e-3x^2 R^2 = 0.83
P < .03
Simpson's (C)
0.60
0.45
0.30
0.15
0.00
0 2 4 6 8 10
ΔT - Daily (C)
c) y = 3.87 - 6.16e-2x R^2 = 0.73
P < .02
Species Diversity (H')
4.0
3.2
2.4
1.6
0.8
0.0
0 6 12 18 24
ΔT - Annual (C)
d) y = 3.47 - 0.101x R^2 = 0.76
P < .01
Species Diversity (H')
4.0
3.2
2.4
1.6
0.8
0.0
0 2 4 6 8 10
ΔT - Daily (C)
e) y = - 5321 + 6244x - 570x^2 R^2 = 0.55
P < .20
Mean Abundance (#/m^2)
30000
24000
18000
12000
6000
0
0 2 4 6 8 10
ΔT- Daily (C)
f) y = 10.88 + 8.74x - 0.83x^2 R^2 = 0.67
P < .11
Species Richness (S)
50
40
30
20
10
0
0 2 4 6 8 10
ΔT- Daily (C)

Figure 14. Regressions of (a) AFDM (g/m^2) to mean biomass (mg/m^2) of macroinvertebrates, (b) chlorophyll a (ug/cm^2) to mean biomass, and (c) AFDM against species diversity (H'). Sample size as in Figure 10. Bars represent +1 SD.


a)
y = 1073.2 - 92.4x R^2 = 0.59
P < .17
Mean Biomass (mg/m^2)
2000
1500
1000
500
0
0
2
4
6
8
10
AFDM (g/m^2)
b)
y = 1194.0 - 496.98x R^2 = 0.52
P < .07
Mean Biomass (mg/m^2)
2000
1500
1000
500
0
0.0
0.4
0.8
1.2
1.6
2.0
Chlorophyll a (µg/cm^2)
c)
y = 4.37 - 0.78x + 7.17e-2x^2 R^2 = 0.63
P < .14
Species Diversity (H')
4.0
3.2
2.4
1.6
0.8
0.0
0
2
4
6
8
10
AFDM (g/m^2)

of temperature variation (Minshall et al. 1985). They also suggest that the pattern shown by Simpson's index in Big Creek are more representative of actual trends than is the pattern shown by H'.

Functional feeding group: numbers vs. habitat factors. A correlation matrix for all the habitat parameters against each functional feeding group expressed as mean numbers also can be found in Table 5. Although the range in velocity values was quite small, the numbers of filterers displayed a weak negative relationship to mean substrate size (Figure 15a). Shredder numbers showed a significant positive trend with increasing CV of velocity, while the numbers of scrapers showed a positive relationship to mean velocity (Figure 15b,c). The number of gatherers responded in a negative fashion to mean velocity (Figure 15d).

Shredder numbers decreased with an increase in depth, while showing an increase in numbers to the CV of depth (Figure 16a,b). Gatherers showed a parabolic but nonsignificant function to increasing depth (Figure 16c). Shredders significantly decreased in numbers as A/A_b or D/D_b increased but the relationship for gatherers tended toward a hyperbolic one (Figure 17a-d). Shredder numbers also displayed a negative function to Delta A (Figure 18a). Although indicated by a relatively high "r^2" value, no obvious ecological relationship was evident for filterer numbers against Delta A (Figure 18b). The numbers of scrapers had a parabolic relationship with increasing Delta A (Figure 18c). The consistent trend of decreasing shredder numbers with the above physical parameters suggests that these parameters may be indicative of the retentive capacity and thus food retaining ability for a site.

Shredder numbers significantly decreased with increasing Delta T-daily and Delta T-annual (Figure 19a,b). This is not surprising because the headwaters of a drainage should not only display the least variation in temperature but also be cool and contain the greatest amount food resource for shredders (Vannote et al. 1980). Scraper numbers displayed a parabolic pattern to Delta T-daily and Delta T-annual (Figure 19c,d), while the number of gatherers displayed just the opposite pattern (Figure 19e,f).

As would be expected, shredder and gatherer numbers significantly increased with an increase in BOM, and they tended to decrease over most of the range of chlorophyll a values (Figure 20a-d). Shredder and scraper numbers displayed nonsignificant relationships to the quantity of AFDM (Figure 20e,f).

Functional feeding group: biomass vs. habitat factors. A correlation matrix of each functional feeding group in terms of biomass against all habitat factors also can be found in Table 5. Although the range in velocity values was quite small, gatherer biomass decreased with an increase in mean velocity (Figure 21a). The biomass of filterers increased with an increase in mean velocity (Figure 21b).

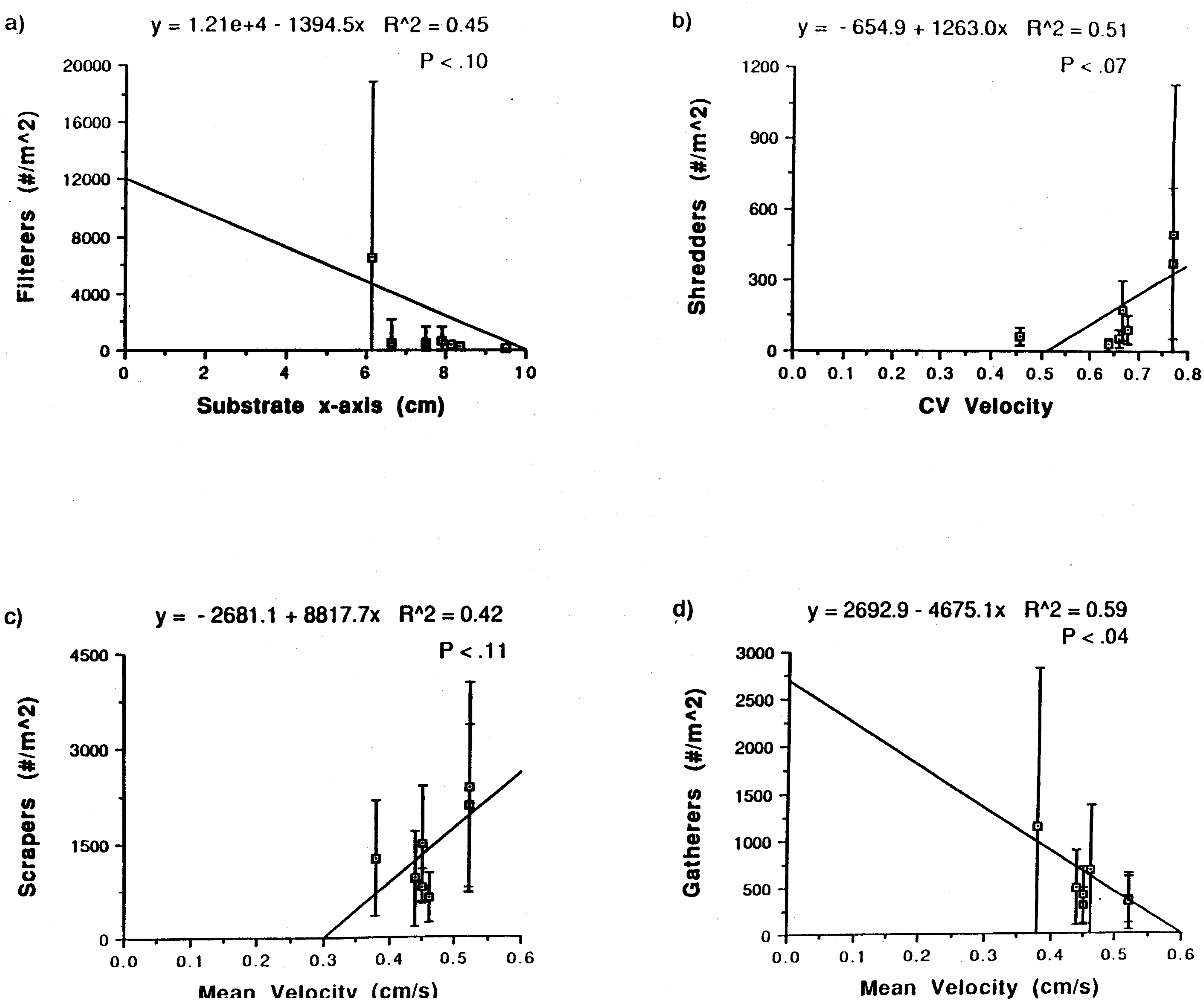
Shredders biomass, as with numbers, significantly decreased with an increase in depth (Figure 22a). Gatherer biomass showed a hyperbolic response to mean depth while showing a nonsignificant increase with the CV of depth (Figure 22b,c). Shredder and gatherer biomass also displayed similar trends, as with numbers,. against A/A_b, and D/D_b. The biomass of shredders and gatherers both significantly decreased in a curvilinear fashion with increases in A/A_b, and D/D_b (Figure 23a-d).

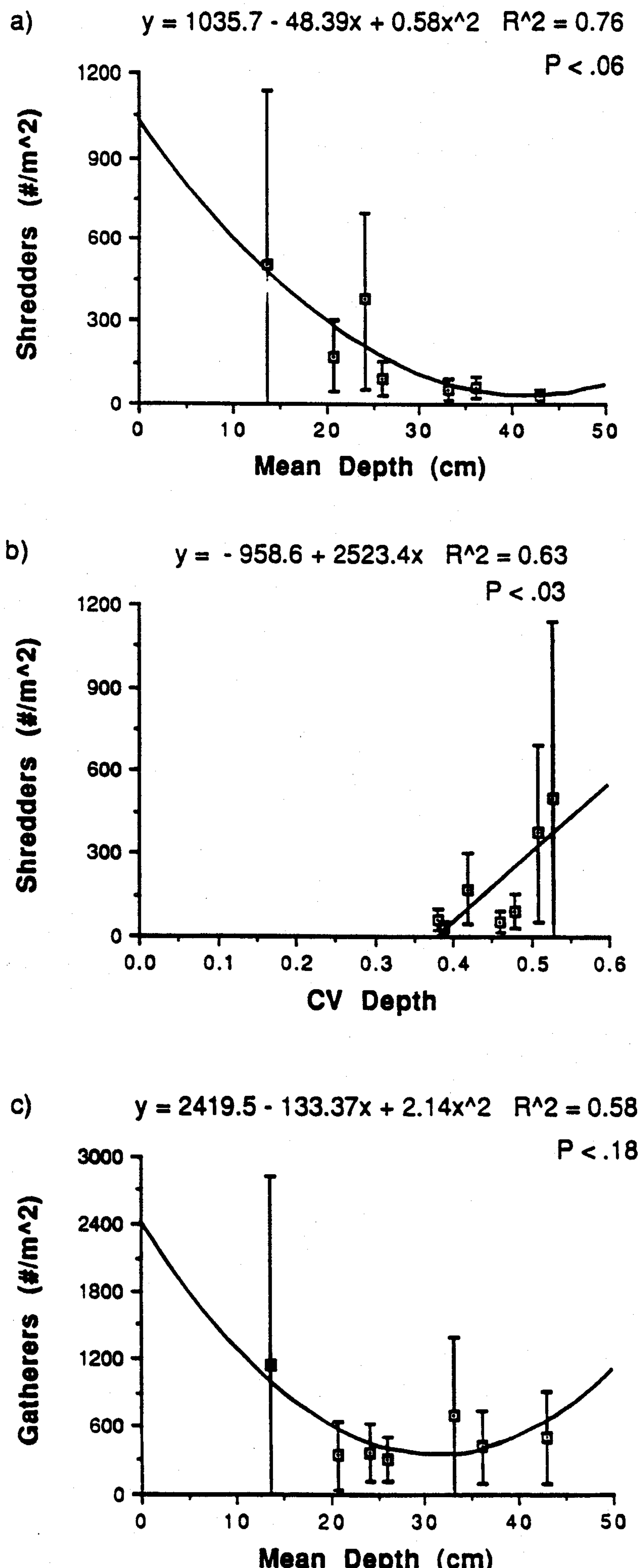
Table 5. Correlation matrix for linear and second-order (*) R^2 values.

Category	Measure	Total#	Total mg	S	H'	C	Abundance values				Biomass values			
							Shred	Filt	Scrap	Gath	Shred	Filt	Scrap	Gath
Substratum	Mean	.31	.66	.02*	.02	.04	.16*	.69*	.33*	.09*	.34*	.34	.27*	.32*
(x-axis)	CV	.13*	.11*	.00*	.07	.12	.16*	.42*	.08*	.30*	.06*	.07	.07*	.08*
Mean Depth	Mean	.20*	.31	.30	.41	.37*	.76*	.12*	.43*	.58*	.92*	.20*	.32*	.88*
	CV	.09*	.04	.07	.49	.57*	.63	.18*	.12*	.44*	.35	.01	.20*	.34
Mean Velocity	Mean	.54	.54	.52	.10	.33	.03	.39*	.81*	.59*	.98*	.55	.14*	.54
	CV	.17*	.17*	.24*	.58*	.14	.93*	.14*	.24*	.22*	.25	.04	.28*	.33*
Discharge	Area (low/high)	.59*	.59	.46*	.27	.48*	.84	.27*	.44*	.77*	.93*	.40*	.37*	.86*
	Depth (low/high	.51*	.40	.30*	.31	.57*	.86	.13*	.24*	.69*	.90*	.24*	.37*	.84*
	ΔArea	.13	.22	.30	.84*	.79*	.55	.57*	.68*	.17*	.26	.60*	.57*	.46*
	ΔDepth	.02	.02	.06	.90*	.85	.45*	.09*	.32*	.00	.14	.06*	.11	.18*
ΔTemperature	ΔAnnual	.32*	.17*	.35*	.73	.71*	.84*	.26*	.54*	.63*	.75*	.51*	.13	.80*
(C)	ΔDaily	.55*	.20*	.67*	.76	.83*	.61	.33*	.79*	.66*	.72*	.64*	.18*	.86*
Food	BOM (g/m^2)	.28*	.21*	.05	.34*	.34	.60	.25*	.15*	.82*	.97	.38*	.03	.90
	CV BOM	.01	.09	.12	.05	.03	.04	.01	.02	.02	.00	.01	.36	.00
	Chloropyhll [a] (µg/cm^2)	.09	.52	.05	.16	.15	.57*	.11*	.21*	.83*	.96*	.12*	.12	.78*
	CV Chlorophyll [a]	.07	.04	.03	.36	.37	.00	.11	.03	.11	.03	.01	.13	.00
	AFDM (g/m^2)	.25	.60	.23	.63*	.25	.72*	.15*	.48	.00	.15	.20*	.67	.24*
	CV AFDM	.35	.06	.01	.71	.81	.10	.34	.10	.04	.11	.29	.04	.17

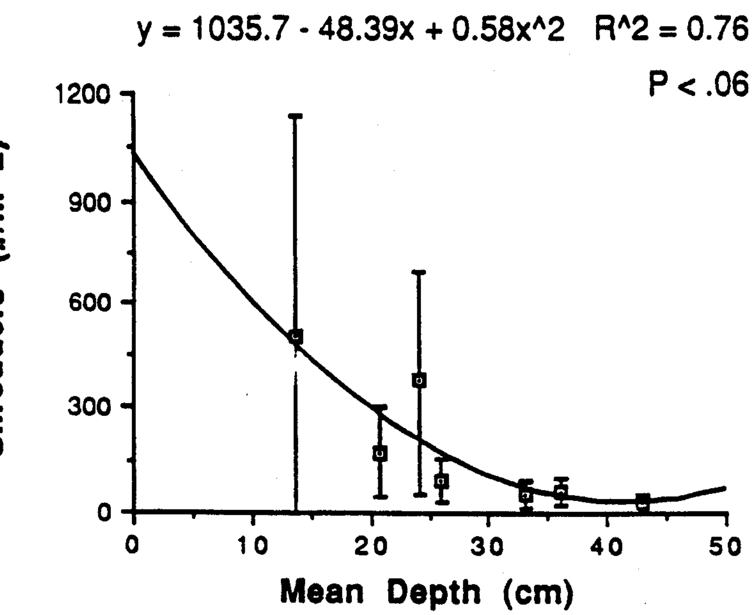
Figure 15. Regressions of (a) substrate x-axis (cm) against mean filterer abundance (#/m^2), (b) the CV of velocity against mean shredder abundance (#/m^2), (c) mean velocity (cm/s) to mean scraper abundance (#/m^2), and (d) mean velocity against mean gatherer abundance (#/m^2). Sample size as in Figure 10. Bars represent +1 SD.

Figure 16. Regressions of (a) mean depth (cm) to mean shredder abundance ($\#/m^2$), (b) the CV of depth to mean shredder abundance, and (c) mean depth against mean gatherer abundance ($\#/m^2$). Sample size as in Figure 10. Bars represent +1 SD.

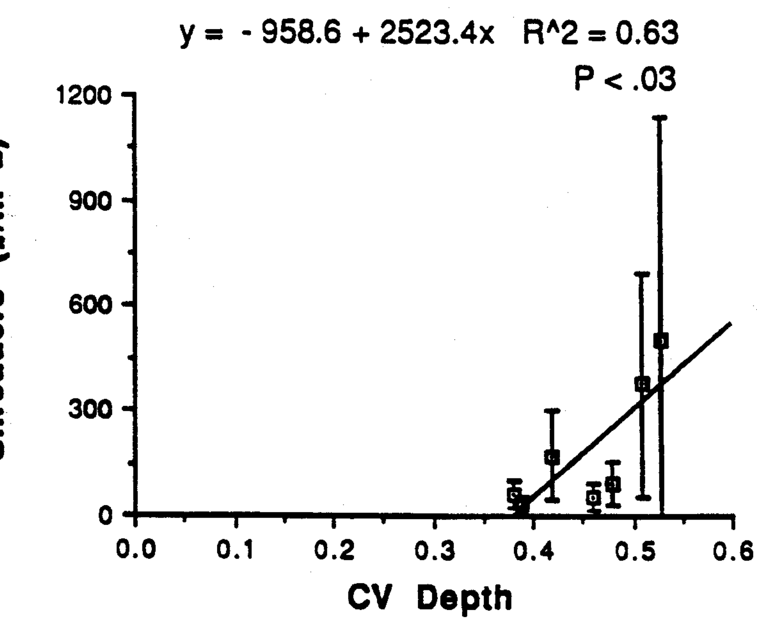

a)
y = 1.21e+4 - 1394.5x R^2 = 0.45
P < .10
Filterers (#/m^2)
Substrate x-axis (cm)
b)
y = - 654.9 + 1263.0x R^2 = 0.51
P < .07
Shredders (#/m^2)
CV Velocity
c)
y = - 2681.1 + 8817.7x R^2 = 0.42
P < .11
Scrapers (#/m^2)
Mean Velocity (cm/s)
d)
y = 2692.9 - 4675.1x R^2 = 0.59
P < .04
Gatherers (#/m^2)
Mean Velocity (cm/s)


a)
y = 1035.7 - 48.39x + 0.58x^2   R^2 = 0.76
P < .06
Shredders (#/m^2)
0
300
600
900
1200
0
10
20
30
40
50
Mean Depth (cm)
b)
y = - 958.6 + 2523.4x   R^2 = 0.63
P < .03
Shredders (#/m^2)
0
300
600
900
1200
0.0
0.1
0.2
0.3
0.4
0.5
0.6
CV Depth
c)
y = 2419.5 - 133.37x + 2.14x^2   R^2 = 0.58
P < .18
Gatherers (#/m^2)
0
600
1200
1800
2400
3000
0
10
20
30
40
50
Mean Depth (cm)

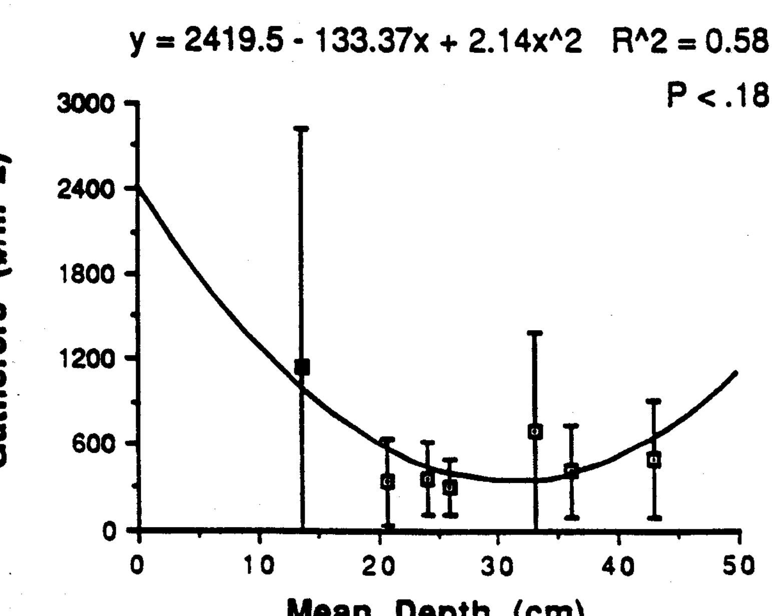
a)

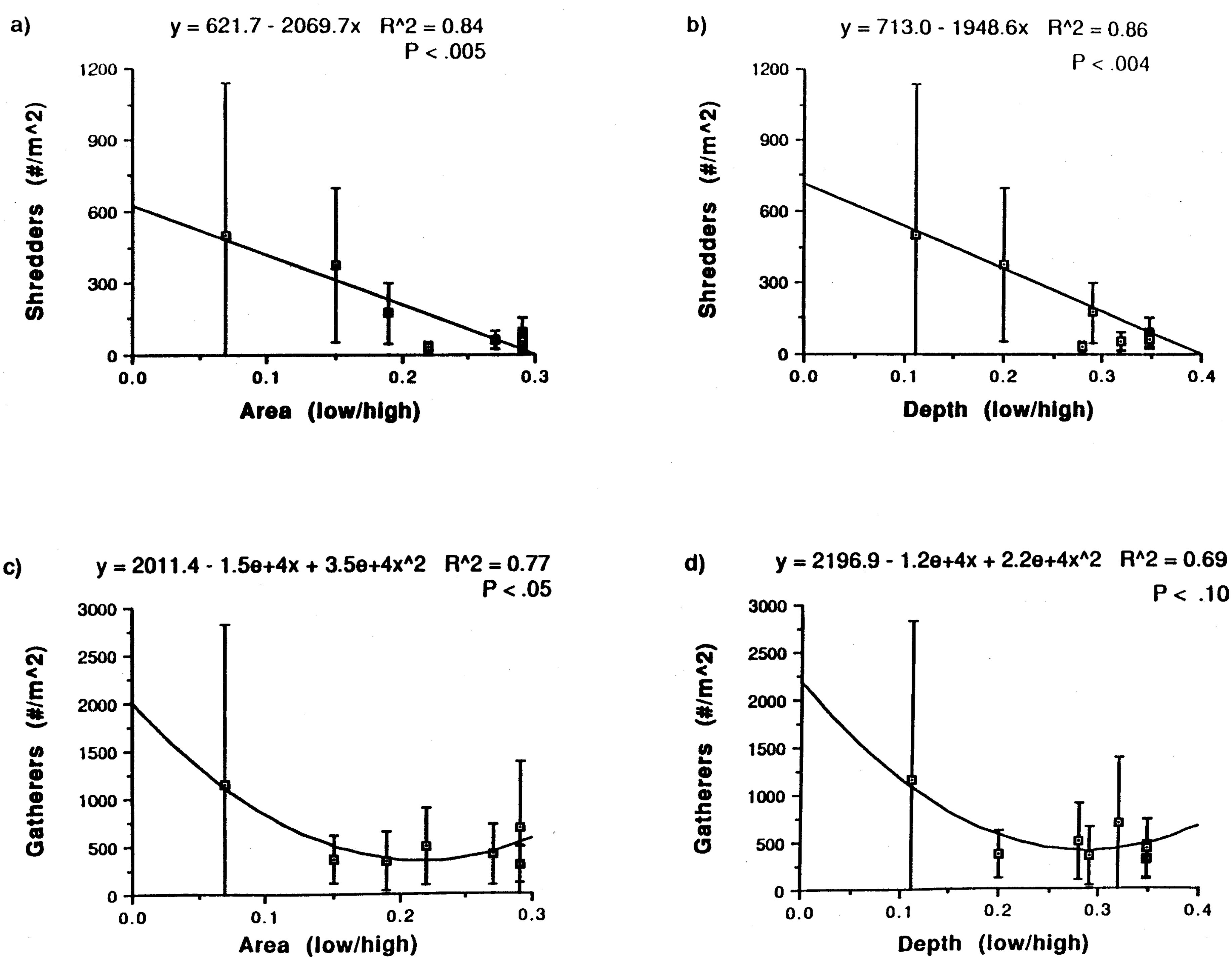

y = 1035.7 - 48.39x + 0.58x^2 R^2 = 0.76
P < .06
Shredders (#/m^2)
1200
900
600
300
0
0
10
20
30
40
50
Mean Depth (cm)

b)

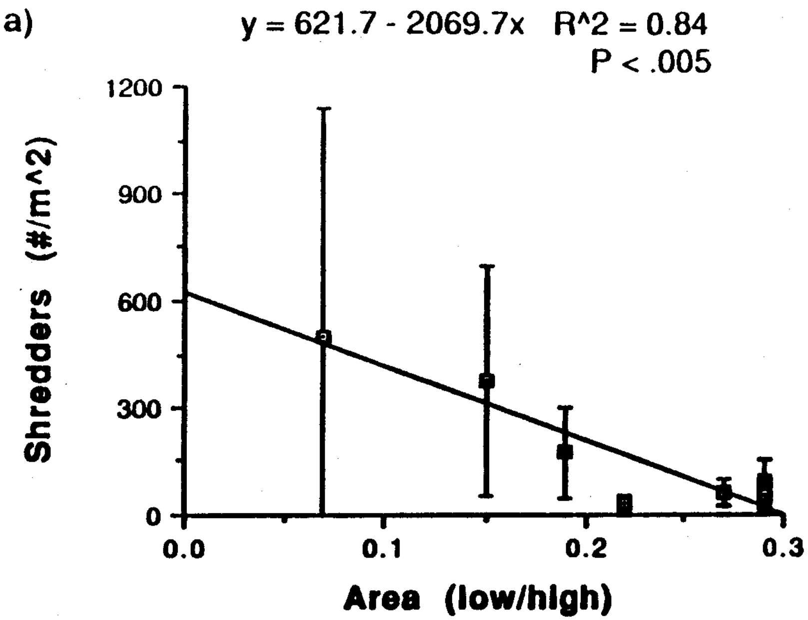

y = - 958.6 + 2523.4x R^2 = 0.63
P < .03
Shredders (#/m^2)
1200
900
600
300
0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
CV Depth

c)

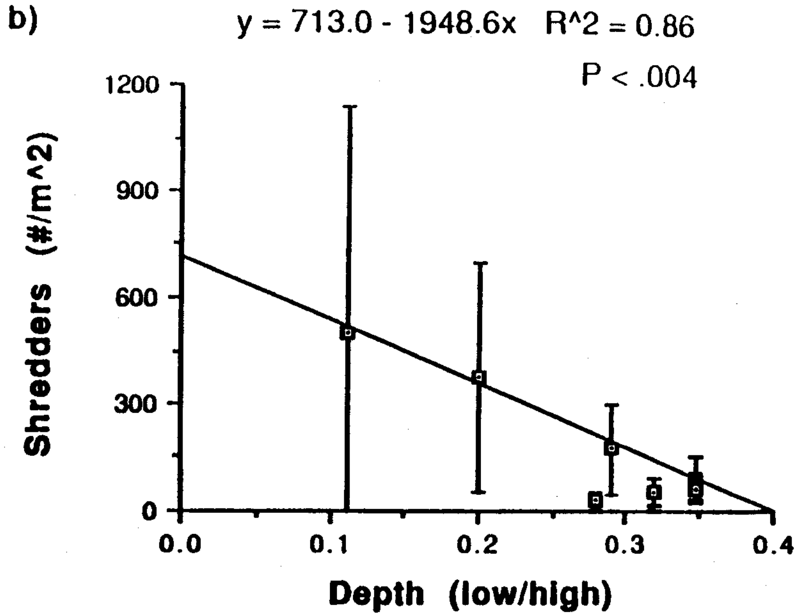

y = 2419.5 - 133.37x + 2.14x^2 R^2 = 0.58
P < .18
Gatherers (#/m^2)
3000
2400
1800
1200
600
0
0
10
20
30
40
50


a)
y = 621.7 - 2069.7x R^2 = 0.84
P < .005
Shredders (#/m^2)
1200
900
600
300
0
0.0
0.1
0.2
0.3
Area (low/high)
b)
y = 713.0 - 1948.6x R^2 = 0.86
P < .004
Shredders (#/m^2)
1200
900
600
300
0
0.0
0.1
0.2
0.3
0.4
Depth (low/high)
c)
y = 2011.4 - 1.5e+4x + 3.5e+4x^2 R^2 = 0.77
P < .05
Gatherers (#/m^2)
3000
2500
2000
1500
1000
500
0
0.0
0.1
0.2
0.3
Area (low/high)
d)
y = 2196.9 - 1.2e+4x + 2.2e+4x^2 R^2 = 0.69
P < .10
Gatherers (#/m^2)
3000
2500
2000
1500
1000
500
0
0.0
0.1
0.2
0.3
0.4
Depth (low/high)

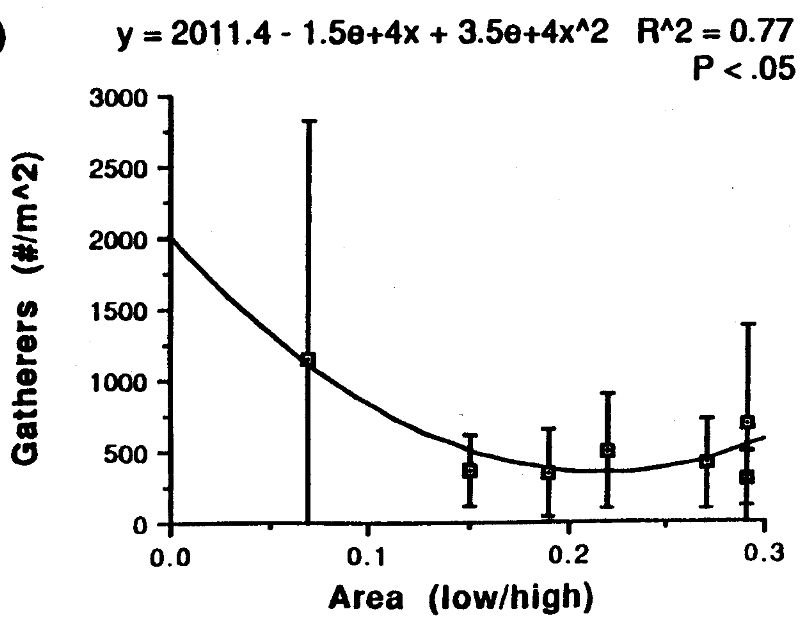
a)


y = 621.7 - 2069.7x R^2 = 0.84
P < .005
Shredders (#/m^2)
1200
900
600
300
0
0.0
0.1
0.2
0.3
Area (low/high)

b)


y = 713.0 - 1948.6x R^2 = 0.86
P < .004
Shredders (#/m^2)
1200
900
600
300
0
0.0
0.1
0.2
0.3
0.4
Depth (low/high)

c)


y = 2011.4 - 1.5e+4x + 3.5e+4x^2 R^2 = 0.77
P < .05
Gatherers (#/m^2)
3000
2500
2000
1500
1000
500
0
0.0
0.1
0.2
0.3
Area (low/high)

d)

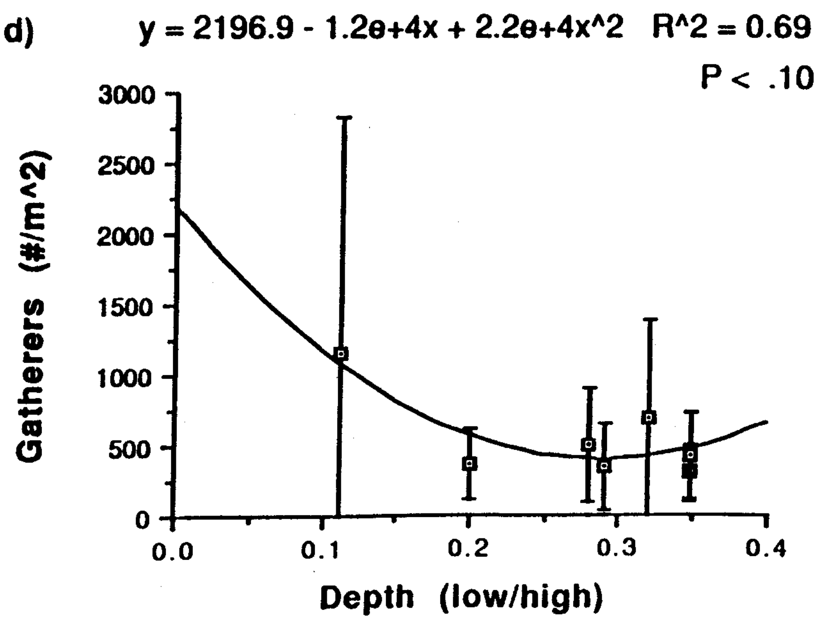
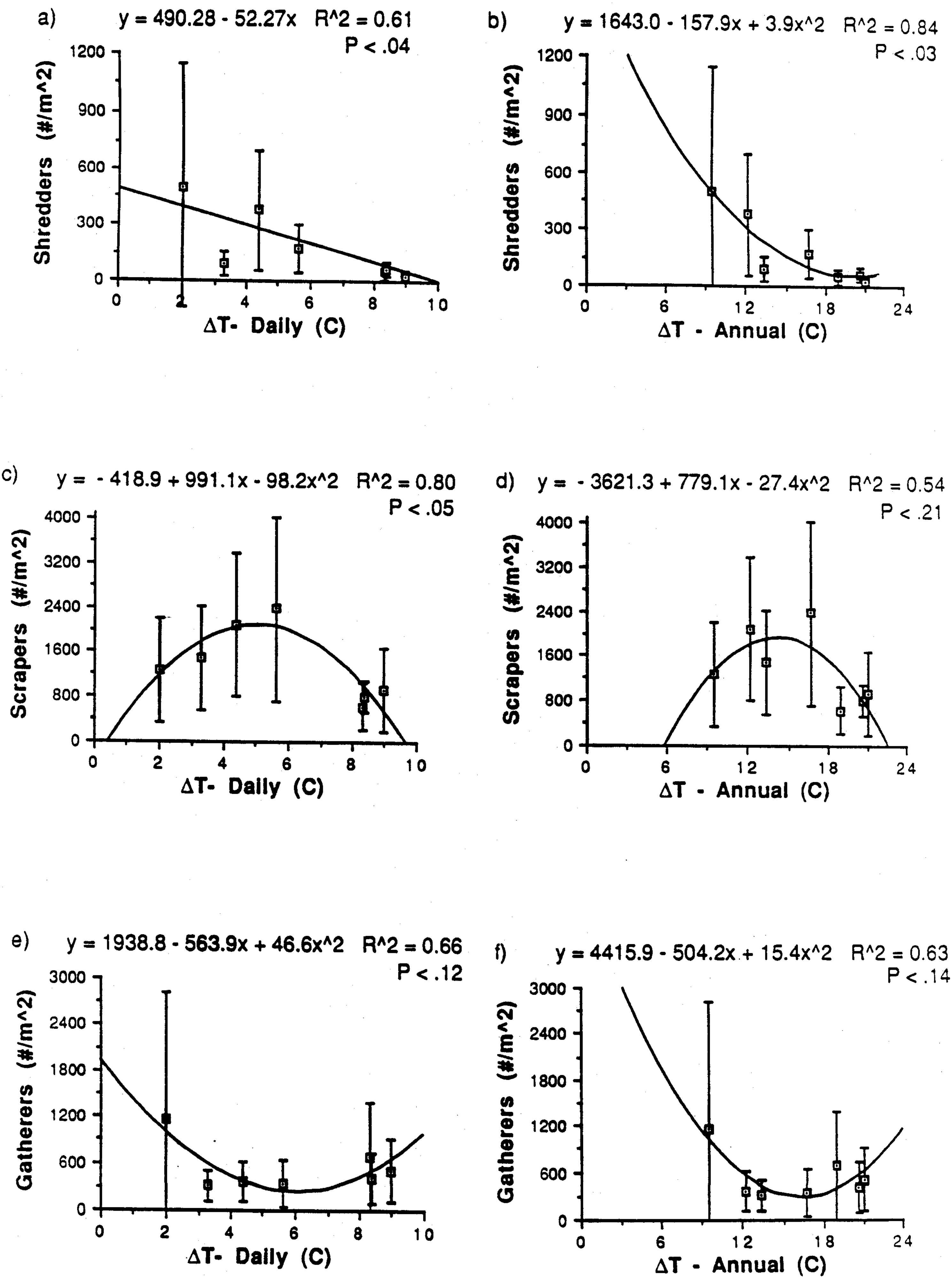

y = 2196.9 - 1.2e+4x + 2.2e+4x^2 R^2 = 0.69
P < .10
Gatherers (#/m^2)
3000
2500
2000
1500
1000
500
0
0.0
0.1
0.2
0.3
0.4
Depth (low/high)

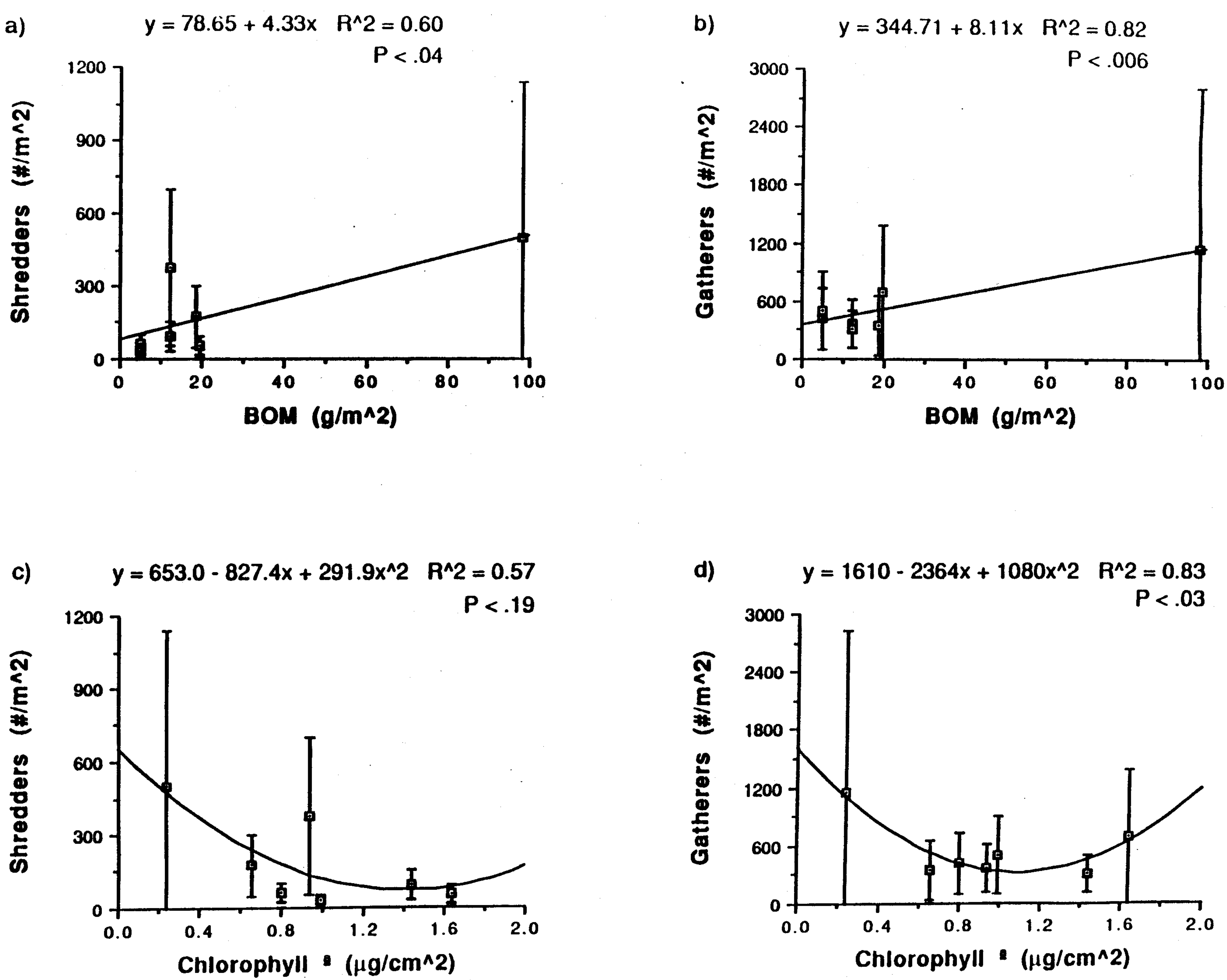
Figure 19. Regressions of (a) daily Delta-T to mean shredder abundance (#/m^2), annual Delta-T to mean shredder abundance, (c) daily Delta-T to mean scraper abundance, (d) annual delta-T to mean scraper abundance, (e) daily Delta-T to mean gatherer abundance, and (f) annual Delta-T to mean gatherer abundance. Delta-T as in figure 5. Sample size as in Figure 10. Bars represent +1 SD.

Figure 19. Regressions of (a) daily Delta-T to mean shredder abundance (#/m^2), annual Delta-T to mean shredder abundance, (c) daily Delta-T to mean scraper abundance, (d) annual delta-T to mean scraper abundance, (e) daily Delta-T to mean gatherer abundance, and (f) annual Delta-T to mean gatherer abundance. Delta-T as in figure 5. Sample size as in Figure 10. Bars represent +1 SD.

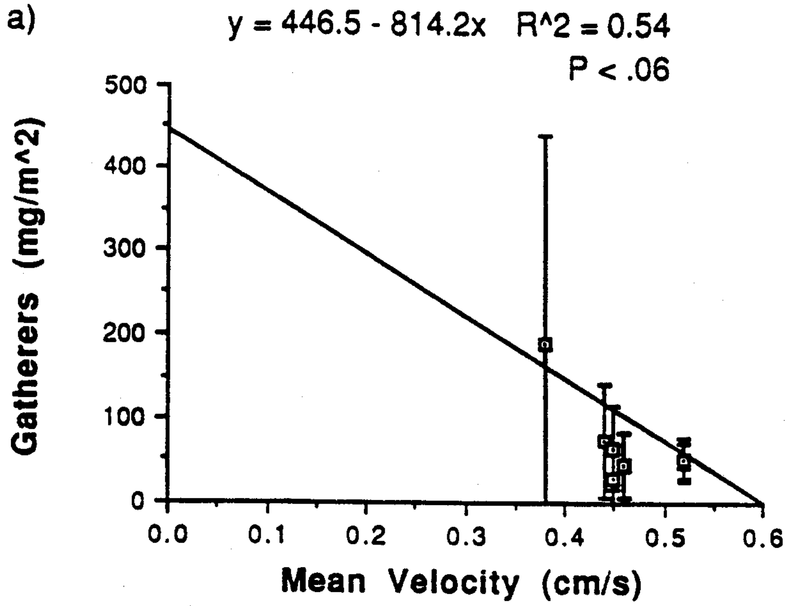


a)
y = 490.28 - 52.27x R^2 = 0.61
P < .04
Shredders (#/m^2)
ΔT- Daily (C)
b)
y = 1643.0 - 157.9x + 3.9x^2 R^2 = 0.84
P < .03
Shredders (#/m^2)
ΔT - Annual (C)
c)
y = - 418.9 + 991.1x - 98.2x^2 R^2 = 0.80
P < .05
Scrapers (#/m^2)
ΔT- Daily (C)
d)
y = - 3621.3 + 779.1x - 27.4x^2 R^2 = 0.54
P < .21
Scrapers (#/m^2)
ΔT - Annual (C)
e)
y = 1938.8 - 563.9x + 46.6x^2 R^2 = 0.66
P < .12
Gatherers (#/m^2)
ΔT- Daily (C)
f)
y = 4415.9 - 504.2x + 15.4x^2 R^2 = 0.63
P < .14
Gatherers (#/m^2)
ΔT - Annual (C)

Figure 20. Regressions of benthic organic matter (BOM: g/m^2) against (a) mean shredder abundance ($\#/m^2$) and (b) mean gatherer abundance; of chlorophyll a (ug/cm^2) against (c) mean shredder and (d) gatherer abundance; and of AFDM (g/m^2) against (e) mean shredder and (f) scraper abundance. Sample size and in Figure 10. Bars represent +1 SD.


a)
y = 78.65 + 4.33x   R^2 = 0.60
P < .04
Shredders (#/m^2)
BOM (g/m^2)
b)
y = 344.71 + 8.11x   R^2 = 0.82
P < .006
Gatherers (#/m^2)
BOM (g/m^2)
c)
y = 653.0 - 827.4x + 291.9x^2   R^2 = 0.57
P < .19
Shredders (#/m^2)
Chlorophyll a (µg/cm^2)
d)
y = 1610 - 2364x + 1080x^2   R^2 = 0.83
P < .03
Gatherers (#/m^2)
Chlorophyll a (µg/cm^2)

a)


y = 446.5 - 814.2x R^2 = 0.54
P < .06
500
400
300
200
100
0
Gatherers (mg/m^2)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Mean Velocity (cm/s)

b)

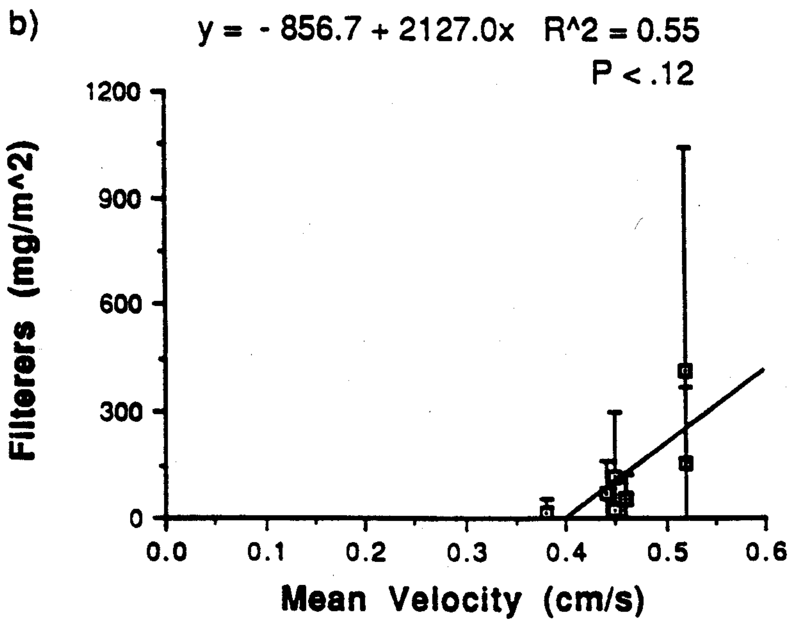

y = - 856.7 + 2127.0x R^2 = 0.55
P < .12
1200
900
600
300
0
Filterers (mg/m^2)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Mean Velocity (cm/s)

Figure 21. Regressions of mean velocity (cm/s) against (a) mean biomass of gatherers (mg/m^2), and (b) mean filterer biomass. Sample size as in Figure 10. Bars represent +1 SD.

Figure 22. Regressions of mean depth (cm) to (a) mean biomass of shredders (mg/m^2), and (b) mean biomass of gatherers; and of the CV of depth against the mean biomass of gatherers. Sample size as in Figure 10. Bars represent +1 SD.

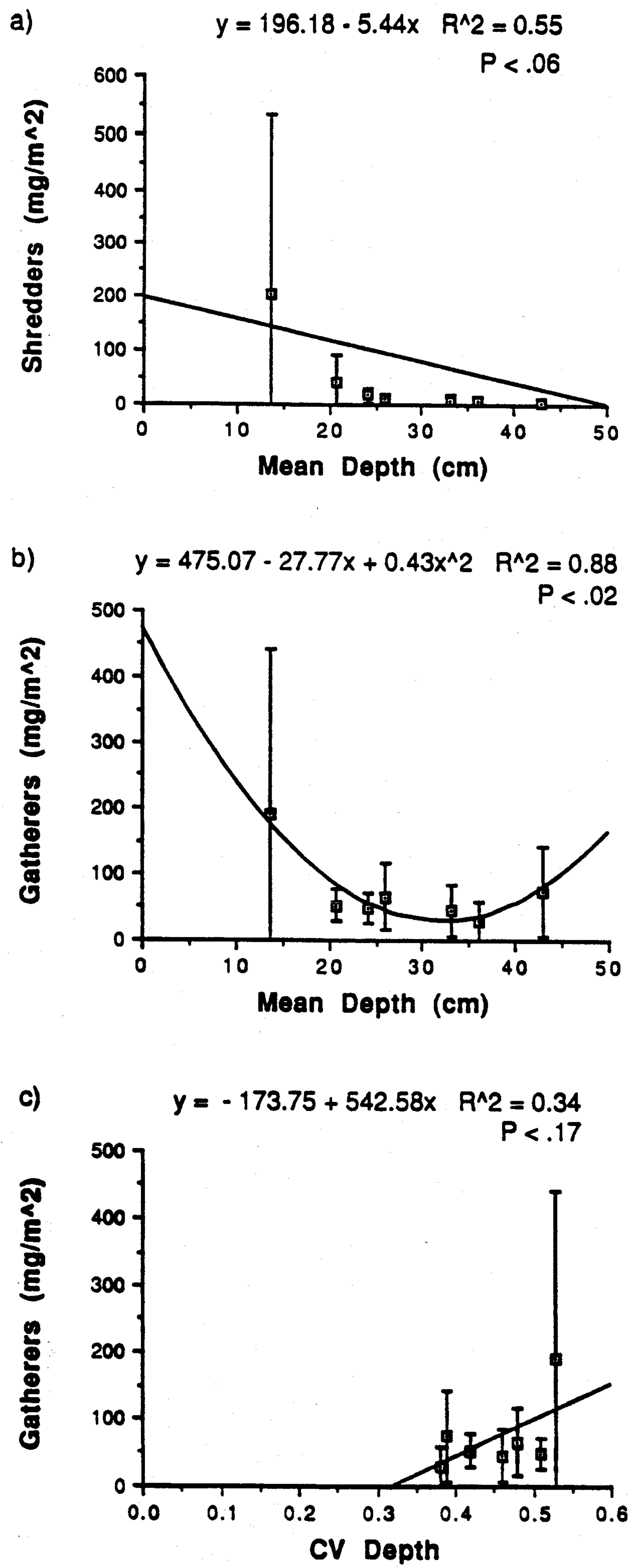
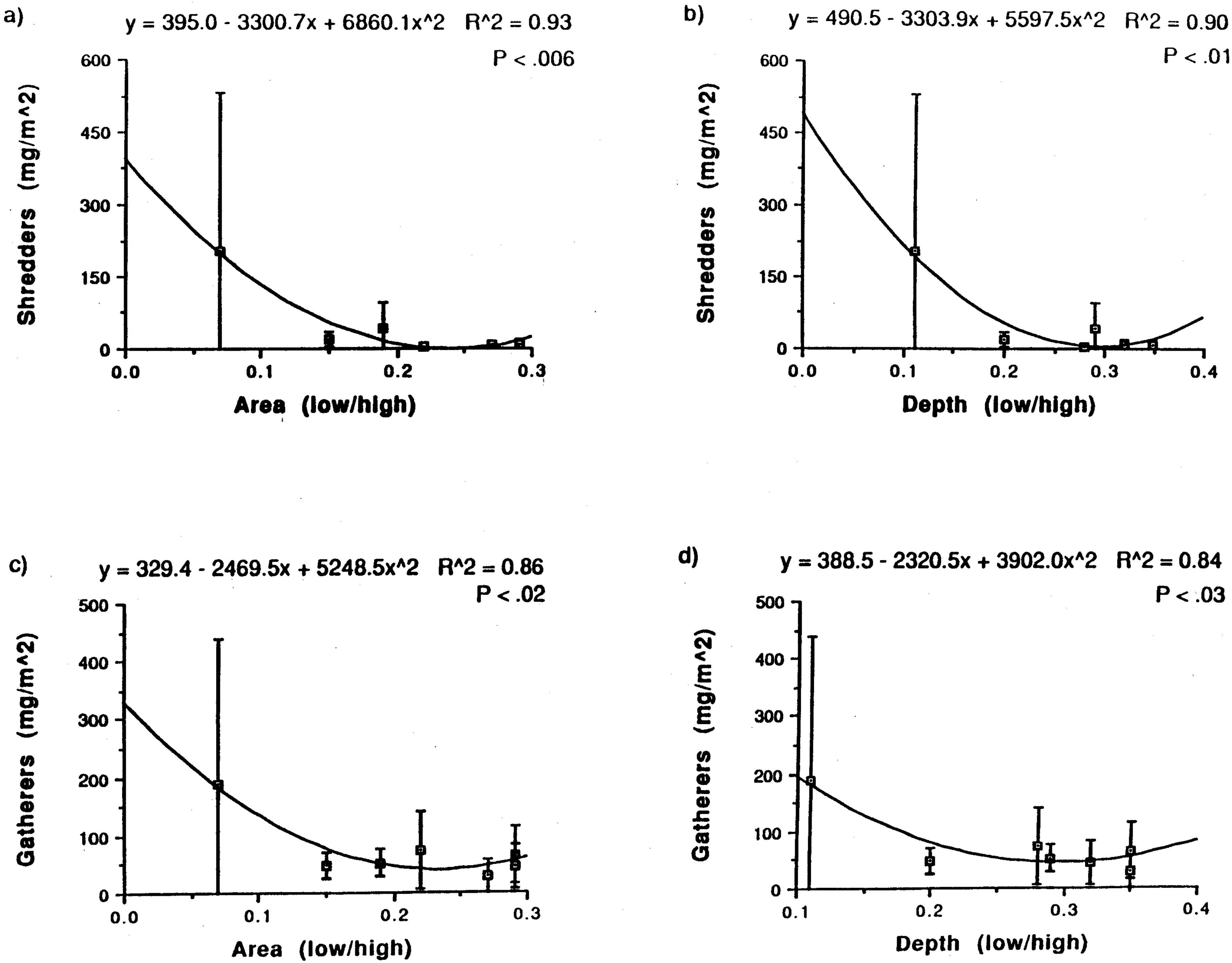

a)
y = 196.18 - 5.44x R^2 = 0.55
P < .06
Shredders (mg/m^2)
600
500
400
300
200
100
0
0
10
20
30
40
50
Mean Depth (cm)
b)
y = 475.07 - 27.77x + 0.43x^2 R^2 = 0.88
P < .02
Gatherers (mg/m^2)
500
400
300
200
100
0
0
10
20
30
40
50
Mean Depth (cm)
c)
y = - 173.75 + 542.58x R^2 = 0.34
P < .17
Gatherers (mg/m^2)
500
400
300
200
100
0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
CV Depth

Figure 23. Regressions of (a) channel area ratio (A/A_b) to mean shredder biomass (mg/m^2), (b) water depth ratio (D/D_b) to mean shredder biomass, (c) A/A_b against the mean biomass of gatherers, and (d) D/D_b to mean gatherer biomass. Ratios as in Figure 4. Sample size as in Figure 10. Bars represent +1 SD.


a)
y = 395.0 - 3300.7x + 6860.1x^2 R^2 = 0.93
P < .006
Shredders (mg/m^2)
600
450
300
150
0
0.0
0.1
0.2
0.3
Area (low/high)
b)
y = 490.5 - 3303.9x + 5597.5x^2 R^2 = 0.90
P < .01
Shredders (mg/m^2)
600
450
300
150
0
0.0
0.1
0.2
0.3
0.4
Depth (low/high)
c)
y = 329.4 - 2469.5x + 5248.5x^2 R^2 = 0.86
P < .02
Gatherers (mg/m^2)
500
400
300
200
100
0
0.0
0.1
0.2
0.3
Area (low/high)
d)
y = 388.5 - 2320.5x + 3902.0x^2 R^2 = 0.84
P < .03
Gatherers (mg/m^2)
500
400
300
200
100
0
0.1
0.2
0.3
0.4
Depth (low/high)

The biomass of scrapers and filterers showed strong but nonsignificant curvilinear relationship to Delta A (Figure 24). Shredder biomass significantly decreased with increasing Delta T-daily and Delta T-annual (Figure 25 a,b). This trend in shredder biomass was similar to the trend in shredder numbers. Filterers displayed nonsignificant parabolic relationships against Delta T-daily and Delta T-annual (Figure 25c,d). Gatherer biomass, as with numbers, significantly decreased with increasing Delta T-daily and Delta T-annual (Figure 25e,f).

Shredder and gatherer biomass significantly increased with increasing BOM biomass (Figure 26a,b). As with numbers, shredder and gatherer biomass significantly decreased with increasing levels of chlorophyll a (Figure 26c,d). The biomass of filterers significantly decreased with increasing AFDM (Figure 26e).

CONCLUSIONS

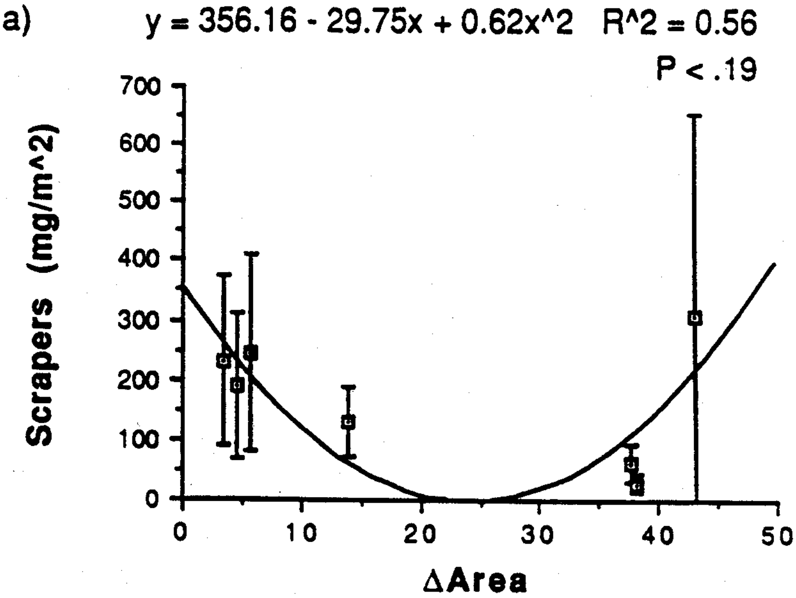
Implications for Future Research

The results of this study suggest that temporal aspects of the habitat templet are more important than within-basin spatial aspects in determining the structure of communities [i.e., temporal heterogeneity is more important than spatial factors in explaining the among-stream differences in community-level measures along a river system]. A logical extension of this finding is that among-stream differences for streams of the same size within a given drainage basin should be much less than along-stream differences because temporal differences in temperature and discharge are likely to be much more similar in the former than in the latter. Implicit in this inference is that streams of the same size (e.g., link number) within a given geoclimatic region will have similar drainage areas, substratum compositions, channel slopes, and the like. These assumptions seem reasonable on the basis of fluvial geomorphology and agree with our cursory observations of Big Creek and similar watersheds within the region. However, one factor that needs to be examined more fully is whether streams of the same size but at different elevations (and hence potentially different temperature and runoff regimes) within a drainage basin exhibit substantially different community-level responses. Obviously in areas of complex geology and/or topography (i.e., heterogeneous basins) the problem becomes more difficult and spatial factors may equal or exceed temporal ones in importance because of the confounding effects of large site-to-site differences in substratum composition, gradient, water chemistry, vegetative cover, etc.

In relatively simple (homogeneous) river basins, in which the normal ecological processes (both terrestrial and aquatic) have been allowed to proceed unregulated by technological humankind over the normal recurrence interval for catastrophic events, it appears that differences in temporal variability will be more important than spatial factors in regulating community response. Futhermore, alterations of the watershed resulting in changes away from the steady state condition should result in a shift in community composition for a given stream size to a state more closely resembling that of a different stream size. For example, burning the vegetation in a watershed of a 2nd order stream should result in increases in the annual amplitudes of temperature and runoff (Minshall et al. 1989). This in turn should cause the community to shift from one like that described in this report (Cliff Creek) to one more closely resembling an intermediate-sized stream in the basin (e.g., Big Creek above Coxey Creek) (i.e., one where the

Figure 24. Regressions of Delta channel area against (a) mean biomass of scrapers (mg/m^2) and (b) mean filterer biomass. Delta refers to the difference between channel area at baseflow to channel area at bankfull. Sample size as in Figure 10. Bars represent +1 SD.

a)


y = 356.16 - 29.75x + 0.62x^2   R^2 = 0.56
P < .19
Scrapers (mg/m^2)
700
600
500
400
300
200
100
0
0
10
20
30
40
50
ΔArea

b)

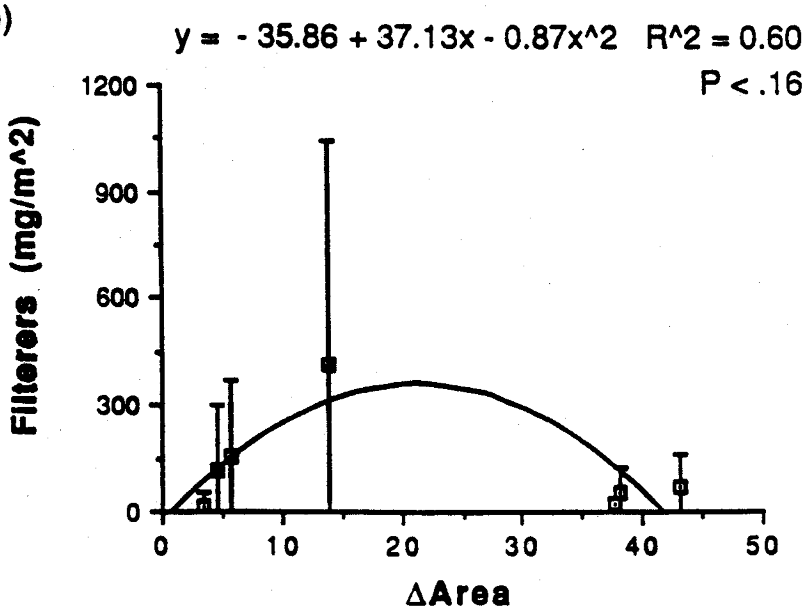

y = - 35.86 + 37.13x - 0.87x^2   R^2 = 0.60
P < .16
Filterers (mg/m^2)
1200
900
600
300
0
0
10
20
30
40
50
ΔArea

Figure 25. Regressions of (a) daily Delta-T (^{o}C) against mean shredder biomass (mg/m^2), (b) annual Delta-T to mean shredder biomass, (c) daily Delta-T to mean filterer biomass, (d) annual Delta-T to mean filterer biomass, (e) daily Delta-T to mean gatherer biomass, and (f) annual Delta-T against mean biomass of gatherers. Delta-T as in Figure 5. Sample size as in Figure 10. Bars represent +1 SD.

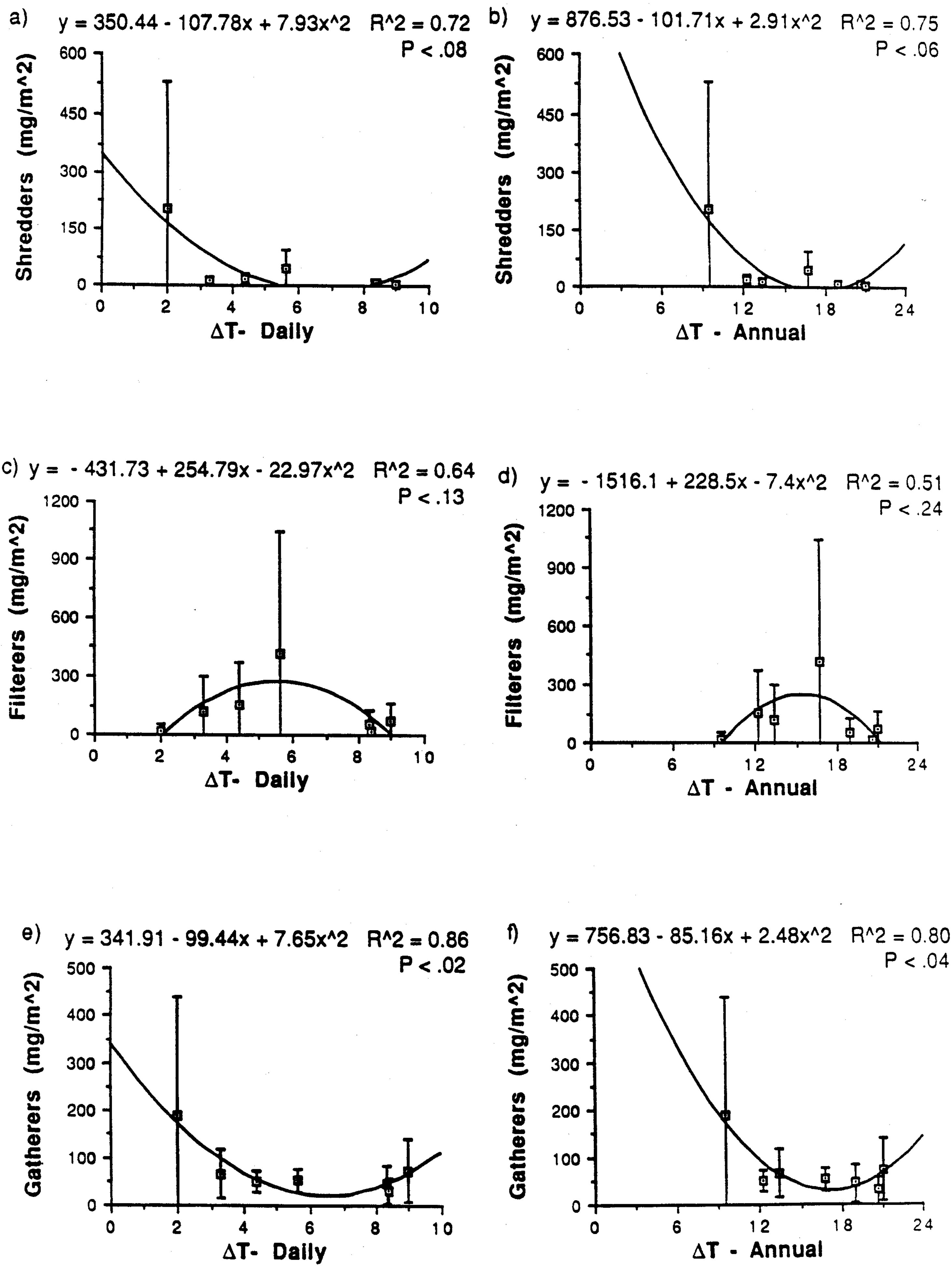
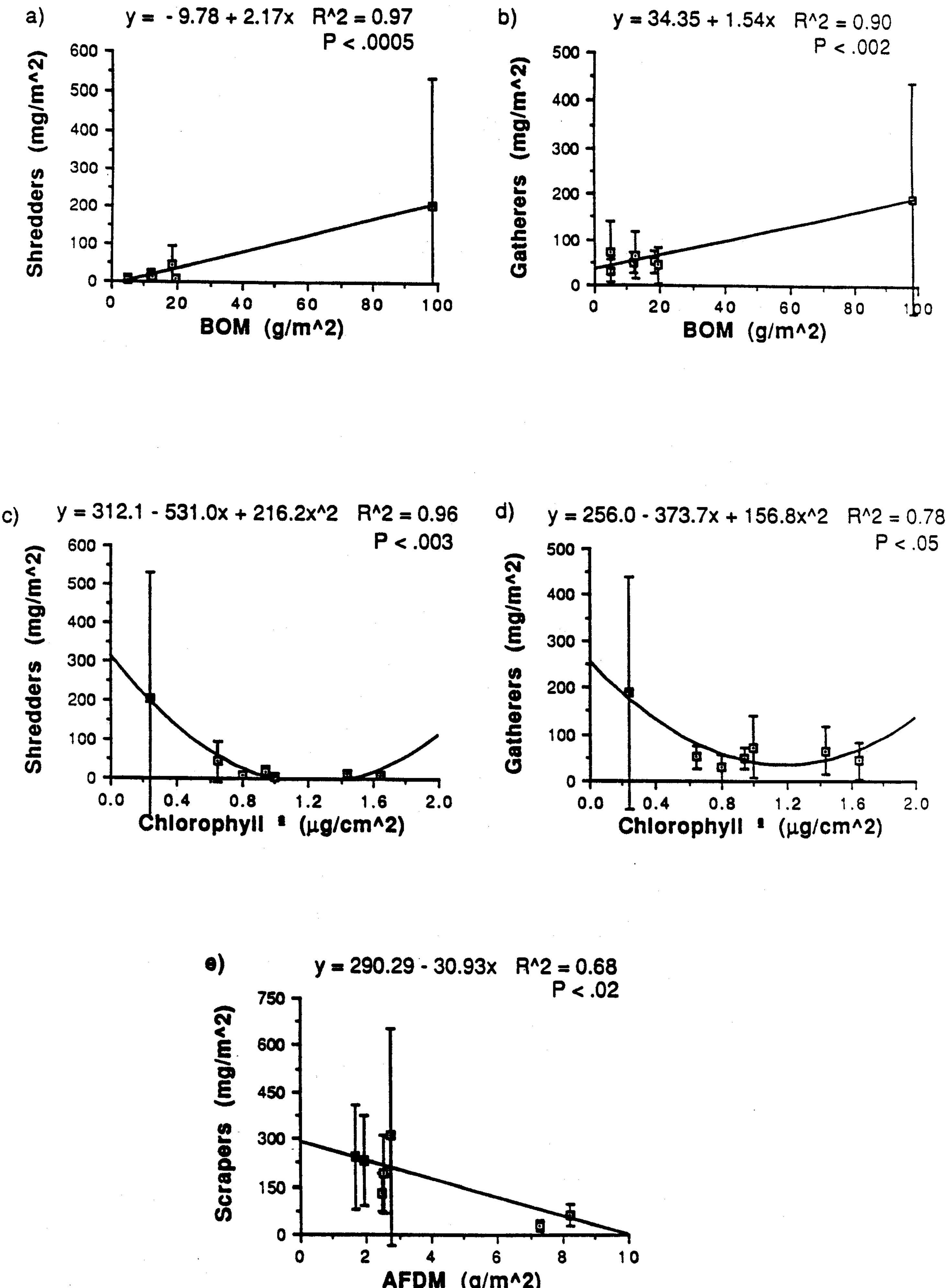

a) y = 350.44 - 107.78x + 7.93x^2 R^2 = 0.72
P < .08
Shredders (mg/m^2)
ΔT- Daily
b) y = 876.53 - 101.71x + 2.91x^2 R^2 = 0.75
P < .06
Shredders (mg/m^2)
ΔT - Annual
c) y = - 431.73 + 254.79x - 22.97x^2 R^2 = 0.64
P < .13
Filterers (mg/m^2)
ΔT- Daily
d) y = - 1516.1 + 228.5x - 7.4x^2 R^2 = 0.51
P < .24
Filterers (mg/m^2)
ΔT - Annual
e) y = 341.91 - 99.44x + 7.65x^2 R^2 = 0.86
P < .02
Gatherers (mg/m^2)
ΔT- Daily
f) y = 756.83 - 85.16x + 2.48x^2 R^2 = 0.80
P < .04
Gatherers (mg/m^2)
ΔT - Annual

Figure 26. Regressions of benthic organic matter (BOM: g/m^2) against (a) mean shredder biomass (mg/m^2) and (b) mean gatherer biomass; of chlorophyll a (ug/cm^2) against (c) mean shredder biomass and (d) mean gatherer biomass; and AFDM (g/m^2) against the mean biomass of scrapers. Sample size as in Figure 10. Bars represent +1 SD.


a)
y = - 9.78 + 2.17x R^2 = 0.97
P < .0005
Shredders (mg/m^2)
BOM (g/m^2)
b)
y = 34.35 + 1.54x R^2 = 0.90
P < .002
Gatherers (mg/m^2)
BOM (g/m^2)
c)
y = 312.1 - 531.0x + 216.2x^2 R^2 = 0.96
P < .003
Shredders (mg/m^2)
Chlorophyll a (µg/cm^2)
d)
y = 256.0 - 373.7x + 156.8x^2 R^2 = 0.78
P < .05
Gatherers (mg/m^2)
Chlorophyll a (µg/cm^2)
e)
y = 290.29 - 30.93x R^2 = 0.68
P < .02
Scrapers (mg/m^2)
AFDM (g/m^2)

temperature and discharge conditions more closely resemble those of the perturbed watershed). A possible way to test this idea would be to examine a number of 10 to 30 link streams in burned and unburned watersheds (or before and after fire) and compare them with communities in 200 to 500 link streams. If our hypothesis is correct, the communities of the burned low link number streams should more closely resemble those of the intermediate link number streams than they do the unburned low link number streams. Over time, the structure of the communities in the burned streams should gradually return to that of communities in the unburned streams (Minshall et al. 1989).

Of the spatial factors evaluated in this study (substratum, velocity, depth, food), the absolute measures were more effective (by a factor of 17 to 11) than the heterogeneity measures in explaining community level responses. Furthermore, most of the stronger absolute-measure correlations were associated with total numbers, total biomass, and richness while most of the stronger heterogeneity-measure correlations where associated with H' and C. Thus, it would appear that in lotic ecosystems it is primarily the aspects of temporal rather than spatial heterogeneity which fit Southwood's (1977) ideas on the habitat templet. Recently Townsend (1989) had made a strong case for the primacy of temporal variation in determining the structure of lotic communities. Our findings and Townsend's ideas support a central feature of the River Continuum Concept that measures of temporal variability such as Delta T (Vannote et al. 1980, Minshall et al. 1983, 1985a) and Delta Q (Minshall et al. 1985b) may largely explain differences in community structure along a river system (see below).

The results of this study also suggest some places where a reduction in effort in the measurement of habitat features can be made with no substantial loss in information. For one, it appears that, in the types of streams studied, water depth is of little or no ecological significance. A distinction here of course is implicit between the depths measured randomly over a reach of stream and those obtained from discrete cross-section transects which can then be used to index changes in discharge. Also, it is evident from our results that only one axis of a rock need be measured in characterizing substratum particle size for ecological purposes or estimation of particle size heterogeneity. The strong correlations between measurements of the x-axis, and those of the y- and z-axes indicates that once the relationships among the three axes are known for a given stream basin, the dimensions of the latter two axes can reliably be derived from measurements of the former. Furthermore, estimates of heterogeneity based on each of the three axes appear to be comparable. However, it does seem that the number of rocks measured can not be reduced appreciably (below 100 per site) and in some cases should be increased. A generally accepted belief among stream ecologists is stream gradient provides a satisfactory index of mean current velocity since a direct correlation between the two is inferred (e.g., Odum 1959). Actually, measurements of bed roughness and hydraulic radius also often are needed to to accurately predict mean velocity (Hynes 1970). Our results indicate no correlation between gradient and velocity.

Relation to the River Continuum Concept

Vannote et al. (1980), based on logic analogous to the intermediate disturbance hypothesis of Connell (1978), postulated that biotic diversity should peak in the mid-reaches of a river system because of the greater diversity (within tolerable limits) of environmental conditions found there. These ideas were subsequently amplified by Ward and Stanford (1983) and Stanford and Ward (1983). In particular, Stanford and Ward assumed that

These ideas were subsequently amplified by Ward and Stanford (1983) and Stanford and Ward (1983). In particular, Stanford and Ward assumed that insect diversity in streams is correlated with temporal environmental heterogeneity and deduced that temperature and discharge were likely to be the most useful measures of such variability. Subsequently, Townsend (1989) has argued that temporal variability is one of the most important factors in structuring stream communities. The results of the present study support several crucial elements of these earlier hypotheses. First, we have shown that, within the same geomorphic region, changes in temperature and discharge are the only major factors to vary predictably and in a parabolic fashion over a broad array of stream sizes. Second, we have shown that most of the conventional measures of community response vary in a similar fashion. Finally, we have demonstrated a stronger correlation between change in temperature and/or discharge and the various community measures than for any other major environmental factor (except total biomass vs. substratum particle size). When we regressed species richness against Delta A plus Delta T_{daily} in a multiple regression the results were highly significant ($r^2 = 0.85$; $p<0.02$). Significant correlations also were found for Simpsons' Index ($r^2 = 0.78$; $p<0.05$) and Shannon-Weiner Diversity ($r^2 = .77$; $p<0.06$). The lack of a significant relationship between total numbers or total biomass and these factors (in combination with any of the factors taken individually) suggest that the factors responsible for determining richness or the apportionment of individuals among taxa are different from (or have a different order of expression than) those which determine total numbers or total biomass (both of which may be as much expressions of biotic production or community function as they are of structure).

Overall patterns of distribution of functional feeding groups were basically the same in terms of either numbers or biomass even though some differences did exist in terms of the finer details (Figures 8,9). Because of this, and because biomass is more meaningful than numbers in terms of functional feeding group trophic partitioning, the discussion here will focus on relationships with respect to biomass. Both shredders and gatherers showed positive correlations with benthic organic matter concentrations (Figure 26). The negative linear correlation between scraper abundance and periphyton standing crops may be a reflection of the fact that the scrapers are strongly keyed on and heavily utilizing this resource at the higher densities of scrapers. Shredders showed strong correlations for a number of other environmental factors besides food but the scrapers and gatherers had higher correlations with food than any other factor (although Delta T was a close second for gatherers)(Table 5). Filterers did not show strong correlations with any of the measures of food abundance but might have if the amounts of seston in the water column, a more direct measure of the food available to them, had been measured.

The River Continuum Concept (RCC) predicts the distribution patterns along a river system for a number of functional feeding groups (FFG's) based on generalizations concerning changes in food quality and quantity with respect to the riparian vegetation, light, and water depth (Vannote et al. 1980). In general, the results for Big Creek support the premises of the relationship between food quality and quantity and FFG responses on which the RCC is based. However, only a few of the actual patterns predicted by the RCC where found in Big Creek. The fact that our study covers only the summer and only the 2nd through 6th orders of a 9th or 10th order river system severely limits evaluation of the FFG aspects of the RCC based on the present study. However, the progressive increase downstream of predators and the lowered abundance of scrapers at several of the larger stream sites were unexpected on the basis of matter (CPOM). CPOM was not differentiated during this study but total BOM, of which it is a component, showed a general downstream decrease. Likewise, the abundances of shredders and BOM were significantly correlated. However, since shredders also were strongly correlated to depth, velocity, discharge, and temperature, the relationship to BOM may have been somewhat fortuitous. Relative biomass of all collectors (gatherers+filterers+miners) ranged from 26 to 49% and showed a parabolic relationship with stream size, peaking at Rush Creek. These results deviate from the pattern predicted by the RCC which assumes a relative constant proportion of benthic invertebrate collectors over the upper to middle reaches of a river system.

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Appendix 1. Mean numbers of individual taxa per square meter (and standard deviations) for study sites in the Big Creek drainage basin of central Idaho in summer 1988.

FFG/Species	Cliff	Beaver	Ramey	Rush	Big/Coxey	Big/Rush	Big/Gorge
Predators							
Acroneuria abnormis						2.1 (4.5)	
Arachnidae				1.1 (3.4)			
Atherix sp.					3.2 (10.1)		
variagata				58.7 (77.8)	37.3 (44.8)	5.3 (10.4)	18.1 (23.6)
Calineuria sp.							2.1 (4.5)
Carabidae						1.1 (3.4)	
Carabidae adult			1.1 (3.4)				
Ceratapogonidae	35.2 (53.7)	1.1 (3.4)	4.3 (10.3)	5.3 (16.9)	1.1 (3.4)	6.4 (16.8)	
Chelifera sp.	2.1 (4.5)	30.9 (33.2)	112.0 (74.3)			4.3 (10.3)	
Chloroperlidae					3.2 (7.2)	1.1 (3.4)	
Claasenia sp.					6.4 (14.4)	10.7 (11.2)	5.3 (9.1)
Cultus sp.		92.8 (51.1)					
Dicronota sp.	2.1 (6.7)		3.2 (5.2)	5.3 (11.5)		1.1 (3.4)	1.1 (3.4)
Doroneuria sp.						3.2 (10.1)	
Dytiscidae				10.7 (33.7)	1.1 (3.4)		10.7 (12.3)
adult				2.1 (6.7)			
Empididae	1.1 (3.4)			61.9 (67.3)	24.5 (26.6)	5.3 (10.4)	7.5 (10.1)
pupae				16.0 (29.4)			
Glutops sp.			58.7 (72.9)				
Haliplus sp.							1.1 (3.4)
Hesperoperla sp.				8.5 (18.7)			
pacifica				92.8 (91.9)	11.7 (19.8)	4.3 (10.3)	
Hexatoma sp.			2.1 (4.5)	18.1 (28.5)	16.0 (23.7)	52.3 (43.7)	54.4 (35.0)
Hydracarina	10.7 (10.1)	96.0 (76.3)	121.6 (83.6)	580.4 (494.6)	318.0 (192.4)	578.3 (377.0)	587.9 (442.6)
Hydrovatus					184.6 (543.5)	4.3 (10.3)	
adult					3.2 (5.2)		
Isoperla sp.			7.5 (14.3)	22.4 (35.0)	3.2 (10.1)		9.6 (13.7)
Ispoperlas sp.					3.2 (10.1)		
Limnia sp.							2.1 (6.7)
Megarcys sp.	27.7 (17.6)	17.1 (16.1)	42.7 (31.4)				1.1 (3.4)
Nematoda	275.3 (833.2)	3.2 (7.2)	61.9 (57.1)	51.2 (52.0)	8.5 (17.3)	71.5 (54.2)	18.1 (19.5)
Oreodytes sp.		1.1 (3.4)		49.1 (101.6)		3.2 (10.1)	6.4 (20.2)

Appendix 1. (continued)

FFG/Species	Cliff	Beaver	Ramey	Rush	Big/Coxey	Big/Rush	Big/Gorge
Perlesta sp.			2.1 (6.7)			19.2 (34.4)	
Perlidae			154.7 (142.6)			36.3 (41.2)	
Perlodidae				3.2 (10.1)	9.6 (16.3)	24.5 (28.0)	12.8 (24.5)
Polymera or Limnephila				3.2 (10.1)			
Plecoptera	25.6 (81.0)	115.2 (150.1)					
Rhyacophila sp.			5.3 (11.5)	2.1 (4.5)		1.1 (3.4)	
angelita	69.4 (112.4)	9.6 (13.7)	186.7 (219.6)		1.1 (3.4)		2.1 (6.7)
bifila		2.1 (4.5)					
hyalinata			23.5 (18.0)		2.1 (6.7)		1.1 (3.4)
oreta		1.1 (3.4)					
rotunda	48.0 (82.5)	13.9 (31.8)					
vaccua		23.5 (25.5)	132.3 (119.5)				
vagrita		5.3 (16.9)	8.5 (20.0)		1.1 (3.4)	4.3 (10.3)	2.1 (6.7)
vepulsa		13.9 (19.5)	127.0 (125.7)	1.1 (3.4)	9.6 (16.3)		2.1 (4.5)
verrula					2.1 (6.7)		
Rickera sp.		7.5 (13.4)					
Skwala sp.					42.7 (65.4)	8.5 (13.1)	27.7 (38.0)
Turbellaria	40.5 (65.2)	87.5 (84.4)	77.9 (66.9)	11.7 (14.6)		1.1 (3.4)	
Gatherers							
Ameletus sp.			1.1 (3.4)	46.9 (148.5)	17.1 (26.7)	7.5 (15.9)	1.1 (3.4)
connectus				2.1 (6.7)			
cooki			10.7 (24.6)		12.8 (40.5)		
oregonesis							1.1 (3.4)
similor				2.1 (6.7)			
siphlonuras				35.2 (58.2)			
sparsatus				2.1 (6.7)			
velox	4.3 (9.0)			2.1 (6.7)			
Ampumixis sp.	5.3 (10.4)						
Antocha sp.	4.3 (7.5)	14.9 (43.6)	6.4 (10.3)	76.8 (167.2)	11.7 (13.7)	1.1 (3.4)	16.0 (26.3)
pupae				2.1 (4.5)			
Aptania sp.	36.3 (34.2)	28.8 (16.7)					
Attenella sp.				8.5 (27.0)	41.6 (36.8)	109.9 (171.5)	80.0 (90.9)
Capniidae	5.3 (9.1)	59.8 (60.6)	46.9 (47.8)				

Appendix 1. (continued)

FFG/Species	Cliff	Beaver	Ramey	Rush	Big/Coxey	Big/Rush	Big/Gorge
Ceraclea sp.						2.1 (4.5)	
Cleptelmis sp.				8.5 (14.0)			
Coleoptera			1.1 (3.4)			1.1 (3.4)	
Collembola			1.1 (3.4)				
Copepoda			63.0 (116.7)			6.4 (20.2)	
Cylloepus sp.							1.1 (3.4)
Diptera			1.1 (3.4)	4.3 (5.5)		1.1 (3.4)	
Dubiraphia sp.					1.1 (3.4)		
Ecclisomyia sp.	1.1 (3.4)	2.1 (6.7)	3.2 (10.1)			10.7 (33.7)	
Ephemera sp.							1.1 (3.4)
Ephemerella sp.	17.1 (54.0)	3.2 (7.2)					
grandis				5.3 (7.5)			
heterocaudata				4.3 (10.3)			
Ephemeroptera			1.1 (3.4)				
Hemerodromia sp.			2.1 (4.5)	1.1 (3.4)		1.1 (3.4)	
pupae				4.3 (10.3)		1.1 (3.4)	
Heterelmis sp.				3.2 (10.1)			
Heterlimnius sp.	387.3 (410.7)	23.5 (16.5)	148.3 (121.1)	28.8 (28.9)	1.1 (3.4)	38.4 (41.2)	39.5 (30.2)
adult	10.7 (14.2)	5.3 (5.6)	7.5 (16.7)	1.1 (3.4)		2.1 (4.5)	4.3 (7.5)
Lepidostoma				24.5 (70.4)	350.0 (312.9)	102.4 (145.8)	146.2 (145.3)
Macromychus sp.			1.1 (3.4)				
Neothremma sp.						1.1 (3.4)	
Ochrotrichia				8.5 (27.0)	8.5 (27.0)		
Optioservus				10.7 (23.0)	30.9 (32.8)	89.6 (89.0)	194.2 (171.7)
adult					5.3 (5.6)	1.1 (3.4)	7.5 (7.2)
Orthotrichia sp.				4.3 (13.5)			
Paraleptophlebia sp.	141.9 (219.5)	1.1 (3.4)	3.2 (5.2)	5.3 (7.5)	4.3 (7.5)	6.4 (13.5)	6.4 (10.3)
Polycentropidae				27.7 (80.5)			
Polycentropus sp.	434.3 (1347.1)	113.1 (89.9)		3.2 (7.2)	1.1 (3.4)		
Psychodidae			6.4 (14.4)				
Rhizelmis sp.				1.1 (3.4)		2.1 (4.5)	
Rhyacophila acropedes	41.6 (67.8)	22.4 (21.0)	12.8 (14.0)	1.1 (3.4)	1.1 (3.4)		
Serratella tibialis	42.7 (70.6)	32.0 (25.6)	53.4 (43.6)	9.6 (10.6)	2.1 (4.5)	14.9 (40.0)	7.5 (13.4)
Stratiomys sp.				4.3 (13.5)			

Appendix 1. (continued)

FFG/Species	Cliff	Beaver	Ramey	Rush	Big/Coxey	Big/Rush	Big/Gorge
Timpanoga sp.					1.1 (3.4)		
Trichoptera			1.1 (3.4)		9.6 (16.3)	6.4 (13.5)	2.1 (6.7)
"A"				2.1 (6.7)	49.1 (87.0)	6.4 (16.8)	
"B"				3.2 (7.2)	108.8 (206.0)	4.3 (13.5)	
"C"				2.1 (6.7)	52.3 (140.2)		
adult	2.1 (4.5)						
pupae	16.0 (36.4)	3.2 (7.2)	2.1 (6.7)				
Tricorythodes sp.						1.1 (3.4)	1.1 (3.4)
Scrapers							
Baetis sp.	312.6 (457.4)						
alexandii						64.0 (108.5)	
bicaudatus				885.6 (1180.8)		65.1 (205.8)	16.0 (50.6)
intermedius				237.9 (282.0)	5.3 (16.9)		6.4 (14.4)
parvus		757.6 (437.3)					
sp. adult		1.1 (3.4)					
tricaudatus			1041.4 (628.1)	491.9 (1421.8)	319.0 (347.2)	436.4 (313.8)	440.7 (609.7)
Blepharicaria				20.3 (43.4)			
Caudatella hystrix			28.8 (43.3)				
Cinygmula sp.	617.8 (334.9)	303.0 (192.9)	85.4 (77.9)	166.5 (122.5)	241.1 (377.2)	37.3 (59.6)	29.9 (46.6)
Deuterophlebia sp.		4.3 (13.5)					
Dioptopsis sp.							3.2 (7.2)
Drunella sp.	25.6 (21.5)			2.1 (6.7)			1.1 (3.4)
colordensis	109.9 (104.1)	8.5 (17.3)	12.8 (14.9)				
doddsi		24.5 (23.1)	52.3 (57.4)	40.5 (72.2)	2.1 (4.5)		
spinifera		3.2 (5.2)	8.5 (11.0)	3.2 (7.2)			
Dactylolabes sp.				1.1 (3.4)			
Deuterophlebia sp.				1.1 (3.4)			
Epeorus sp.					1.1 (3.4)	1.1 (3.4)	
albertae					1.1 (3.4)	17.1 (47.0)	16.0 (24.3)
deceptivus			139.8 (115.5)	34.1 (72.0)		1.1 (3.4)	10.7 (15.1)
longimanus	188.9 (228.4)	388.4 (371.4)	56.6 (50.6)	22.4 (29.9)		2.1 (4.5)	

Appendix 1. (continued)

FFG/Species	Cliff	Beaver	Ramey	Rush	Big/Coxey	Big/Rush	Big/Gorge
Ephemerella sp.					3.2 (7.2)		
aurivilli						70.4 (100.5)	
heterocaudatus		1.1 (3.4)					
inermis		2.1 (4.5)	239.0 (294.2)	4.3 (13.5)	10.7 (33.7)	2.1 (6.7)	2.1 (6.7)
margarita				81.1 (119.3)			13.9 (43.9)
Glossosoma sp.	8.5 (14.0)		2.1 (6.7)	11.7 (23.3)		11.7 (15.5)	4.3 (10.3)
Gordiidae				3.2 (10.1)			
Helichus sp. adult						8.5 (14.0)	
Heptageniidae			324.4 (292.7)	1.1 (3.4)		7.5 (17.5)	1.1 (3.4)
Hydroptila sp.				354.2 (392.6)	8.5 (13.1)	9.6 (9.3)	40.5 (37.6)
pupae				3.2 (10.1)		4.3 (13.5)	1.1 (3.4)
Lymnae						39.5 (73.1)	262.5 (634.2)
Neophylax sp.	4.3 (7.5)			1.1 (3.4)			
Ologophlebodes sp.			25.6 (48.3)				
Philourons californicus				7.5 (23.6)			
Physidae						21.3 (37.3)	88.6 (152.3)
Rhithrogena sp.			76.8 (86.8)	4.3 (13.5)		17.1 (20.2)	1.1 (3.4)
Tadpole			1.1 (3.4)				
Taenyopterygidae				2.1 (6.7)			
Shredders							
Alloperla sp.	345.7 (351.5)	38.4 (42.1)	70.4 (79.6)	72.6 (88.0)	28.8 (41.2)	52.3 (41.3)	21.3 (20.1)
Capnia sp.	19.2 (57.1)			1.1 (3.4)			1.1 (3.4)
Clostoeca sp.	1.1 (3.4)						
Lara				5.3 (10.4)			
Limnephila sp.				7.5 (11.3)			
Limnephilus sp.				16.0 (16.9)			
Limnephilidae			61.9 (80.0)			5.3 (13.5)	
Limnephilidae pupae			1.1 (3.4)				
Micrasema sp.	12.8 (28.8)	2.1 (4.5)	26.7 (66.2)		3.2 (10.1)		
Nemoura sp.			105.6 (140.2)	4.3 (13.5)			
Pteronarcella sp.				6.4 (14.4)			1.1 (3.4)
Pteronarcys californicus				2.1 (6.7)	13.9 (11.3)	3.2 (5.2)	3.2 (5.2)
Tipula sp.	14.9 (18.3)	1.1 (3.4)		3.2 (7.2)			1.1 (3.4)

Appendix 1. (continued)

FFG/Species	Cliff	Beaver	Ramey	Rush	Big/Coxey	Big/Rush	Big/Gorge
Visoka cataractae			1.1 (3.4)				
Yoroperla brevis	1.1 (3.4)		1.1 (3.4)				
Zapada sp.	108.8 (223.0)			14.9 (25.2)	2.1 (6.7)	1.1 (3.4)	
cinctipes					4.3 (13.5)		
columbiana							
oregonesis		50.1 (37.7)	109.9 (77.9)	40.5 (88.0)			
Filterers							
Arctopsyche sp.	1.1 (3.4)	66.2 (103.8)		39.5 (72.6)			
grandis		8.5 (12.1)			19.2 (35.9)	2.1 (6.7)	44.8 (103.7)
Brachycentrus sp.		4.3 (7.5)	2.1 (4.5)	192.1 (509.3)	278.5 (344.3)	17.1 (24.2)	2.1 (4.5)
pupae				1.1 (3.4)			
Cladocera			90.7 (230.2)				
Dolophilodes sp.						5.3 (16.9)	
Hydropsyche sp.		18.1 (33.4)	1.1 (3.4)	73.6 (100.8)	12.8 (22.9)	88.6 (113.8)	86.4 (115.7)
Hydropsychidae				36.3 (76.6)		29.9 (46.3)	144.0 (324.5)
Ogiloplectrum sp.				115.2 (184.7)			4.3 (13.5)
Ostracoda	273.2 (863.8)	6.4 (16.8)		18.1 (53.7)		2.1 (6.7)	
Parapsyche sp.			147.2 (125.3)				
elis			6.4 (7.5)				17.1 (54.0)
Simulium sp.	284.9 (771.6)	468.4 (1058.1)	63.0 (103.6)	3062.7 (12321.6)	27.7 (47.5)	16.0 (12.6)	373.5 (845.7)
adult							
pupae		1.1 (3.4)					2.1 (6.7)
Miners							
Chironomidae	353.2 (476.6)	1536.5 (1547.3)	911.2 (842.9)	3035.6 (1726.0)	3435.7 (2892.5)	2091.3 (1139.3)	3245.8 (2478.6)
adult		9.6 (30.4)	4.3 (9.0)			17.1 (20.9)	
pupae	7.5 (13.4)	41.6 (37.8)	154.7 (109.8)	75.8 (84.7)	4.3 (13.5)	95.0 (92.5)	38.4 (110.7)
Lumbriculus sp.	18.1 (25.7)				1.1 (3.4)		
Tubificidae	2116.9 (2619.3)	848.3 (892.7)	5502.5 (4249.0)	1525.8 (2061.7)	169.7 (176.6)	1.1 (3.4)	507.9 (557.7)

Appendix 1. (continued)

FFG/Species	Cliff	Beaver	Ramey	Rush	Big/Coxey	Big/Rush	Big/Gorge
Others							
Ceraclea sp.							2.1 (6.7)
Helichus adult				1.1 (3.4)			
Molanna sp.		12.8 (28.8)		43.7 (70.3)			44.8 (120.9)
Pupae, unknown				1.1 (3.4)			
Pseudoscorpion	1.1 (3.4)						
Tadpole	2.1 (6.7)						
Tres sp.							3.2 (10.1)
Terrestrials	13.9 (19.5)	34.1 (21.2)	53.4 (49.3)	24.5 (56.0)		6.4 (13.5)	
Wormaldia			99.2 (165.9)				

ppendix 2. Mean biomass of individual taxa per square meter (and standard deviations) for study sites in the Big Creek drainage basin of central Idaho in summer 1988.

FG/Species	Cliff Creek	Beaver Creek	Ramey Creek	Rush Creek	Big/Coxey	Big/Rush	Big/Gorge
redators							
croneuria abnormis						8.93 (20.93)	
rachnidae				0.07 (0.21)			
therix sp.					4.25 (13.44)		
variagata				124.22 (198.39)	15.28 (30.75)	6.20 (13.07)	12.98 (25.93)
alineuria sp.							3.28 (10.38)
arabidae			0.83 (2.62)			0.11 (0.34)	
arabidae adult							
eratapogonidae	6.58 (13.20)	0.12 (0.37)	0.42 (1.00)	12.36 (39.08)	0.07 (0.23)	0.15 (.34)	
helifera sp.	0.17 (0.36)	2.77 (3.43)	7.03 (4.39)			1.10 (2.69)	
hloroperlidae					0.06 (0.14)	0.04 (0.11)	
laasenia sp.					3.15 (6.80)	30.37 (56.95)	25.33 (68.97)
ultus sp.		1.07 (0.71)					
icronota sp.	0.04 (0.14)		0.05 (0.08)	1.04 (2.81)		0.06 (0.19)	0.04 (0.13)
oroneuria sp.						0.44 (1.40)	
ytiscidae				0.31 (0.99)	0.06 (0.18)		1.37 (1.78)
adult				2.08 (6.57)			
mpididae	0.03 (0.09)			10.38 (14.32)	3.21 (2.94)	0.86 (1.47)	2.40 (3.88)
pupae				3.63 (5.63)			
lutops sp.			21.24 (26.04)				
aliplus sp.							1.28 (4.03)
esperoperla sp.				15.01 (40.79)			
pacifica				144.32 (224.29)	44.65 (135.83)	10.61 (26.89)	
exatoma sp.			0.40 (0.85)	52.99 (56.58)	36.11 (51.81)	119.19 (144.27)	156.50 (171.01)
ydracarina	0.82 (1.17)	3.61 (3.80)	2.89 (2.54)	19.33 (19.43)	9.54 (5.80)	11.38 (5.56)	18.61 (15.85)
ydrovatus					3.56 (9.07)	0.26 (0.72)	
adult					1.92 (4.06)		
soperla sp.			10.00 (17.94)	1.05 (1.43)	0.34 (1.07)		0.65 (1.37)
spoperlas sp.					0.02 (0.05)		
imnia sp.							5.60 (17.70)
egarcys sp.	23.39 (20.70)	3.88 (5.95)	17.62 (14.48)				0.15 (0.48)
ematoda	1.66 (4.31)	0.26 (0.55)	1.12 (0.69)	4.35 (5.98)	0.45 (1.08)	1.57 (1.12)	1.29 (1.23)
reodytes sp.		0.01 (0.04)		2.16 (4.90)		0.10 (0.31)	0.91 (2.87)
erlesta sp.			0.17 (0.52)			4.08 (10.65)	

Appendix 2. (continued)

FFG/Species	Cliff Creek	Beaver Creek	Ramey Creek	Rush Creek	Big/Coxey	Big/Rush	Big/Gorge
Perlidae			1.86 (1.82)			1.82 (2.16)	
Perlodidae				0.10 (0.33)	0.42 (0.72)	1.29 (1.53)	0.43 (0.71)
Polymera or Limnephila				0.60 (1.89)			
Plecoptera	0.39 (1.24)	1.20 (1.49)					
Rhyacophila sp.			14.50 (30.84)	0.06 (0.15)		0.09 (0.28)	
angelita	4.49 (7.25)	1.75 (2.71)	11.19 (12.48)		4.23 (13.38)		0.10 (0.32)
bifila		3.14 (7.90)					
hyalinata			0.91 (0.71)		0.04 (0.11)		0.38 (1.20)
oreta		0.18 (0.56)					
rotunda	3.95 (6.94)	1.48 (4.24)					
vaccua		15.20 (20.62)	29.01 (37.87)				
vagrita		0.09 (0.30)	1.05 (2.39)		0.03 (0.08)	0.09 (0.24)	0.05 (0.15)
vepulsa		1.13 (1.54)	11.64 (11.50)	0.02 (0.06)	0.16 (0.29)		0.08 (0.18)
verrula					0.06 (0.18)		
Rickera sp.		12.75 (20.21)					
Skwala sp.					2.57 (2.91)	1.14 (1.81)	3.92 (4.85)
Turbellaria	21.56 (34.61)	20.54 (19.55)	17.82 (16.47)	3.07 (4.10)		0.03 (0.09)	
Gatherers							
Ameletus sp.			0.03 (0.11)	7.65 (24.18)	1.18 (1.48)	0.17 (0.44)	0.06 (0.20)
connectus				0.51 (1.61)			
cooki			2.58 (8.01)		1.10 (3.47)		
oregonesis							0.00 (0.00)
similor	0.54 (1.21)			0.28 (0.90)			
siphlonuras				7.23 (12.92)			
sparsatus				1.14 (3.60)			
velox				0.00 (0.00)			
Ampumixis sp.	28.78 (66.76)						
Antocha sp.	0.06 (0.10)	0.23 (0.66)	0.26 (0.41)	2.26 (4.09)	0.50 (0.73)	0.01 (0.02)	1.29 (1.72)
pupae				0.80 (1.69)			
Aptania sp.	1.21 (2.66)	0.35 (0.27)					
Attenella sp.				0.70 (2.21)	7.89 (12.88)	14.02 (22.03)	30.76 (39.12)
Capniidae	0.44 (0.86)	1.87 (2.02)	2.09 (2.80)				
Ceraclea sp.						0.06 (0.15)	
Cleptelmis sp.				1.71 (2.68)			
Coleoptera			0.10 (0.31)			0.30 (0.93)	

Appendix 2. (continued)

FFG/Species	Cliff Creek	Beaver Creek	Ramey Creek	Rush Creek	Big/Coxey	Big/Rush	Big/Gorge
Collembola			0.01 (0.03)				
Copepoda			0.56 (0.88)			0.03 (0.09)	
Cylloepus sp.							0.00 (0.00)
Diptera			0.02 (0.06)	1.64 (2.82)		0.11 (0.35)	
Dubiraphia sp.					1.14 (3.61)		
Ecclisomyia sp.	0.04 (0.12)	0.13 (0.43)	0.05 (0.15)			0.04 (0.12)	
Ephemera sp.							0.46 (1.46)
Ephemerella sp.	0.15 (0.46)	0.05 (0.15)					
grandis				3.04 (8.76)			
heterocaudata				2.58 (6.17)			
Ephemeroptera			0.86 (2.72)				
Hemerodromia sp.			0.30 (0.65)	0.00 (0.00)		0.16 (0.51)	
pupae				0.93 (2.21)		0.24 (0.76)	
Heterelmis sp.				1.26 (3.97)			
Heterlimnius sp.	36.38 (36.37)	2.69 (2.61)	14.43 (13.26)	4.32 (4.48)	0.07 (0.22)	1.96 (2.17)	4.17 (4.11)
adult	3.87 (5.38)	1.93 (2.20)	2.92 (6.64)	0.32 (1.00)		0.87 (1.86)	2.60 (5.40)
Lepidostoma				1.06 (3.01)	26.61 (35.79)	1.71 (2.12)	3.25 (3.74)
Macromychus sp.			0.23 (0.71)				
Neothremma sp.						0.02 (0.05)	
Ochrotrichia				0.94 (2.97)	0.94 (2.97)		
Optioservus				3.74 (10.26)	1.22 (1.14)	5.38 (5.91)	15.41 (11.51)
adult					1.30 (1.54)	0.33 (1.06)	3.20 (3.63)
Orthotrichia sp.				0.41 (1.30)			
Paraleptophlebia sp.	4.83 (7.22)	0.06 (0.20)	0.09 (0.18)	1.03 (2.44)	0.15 (0.27)	0.36 (0.69)	0.36 (0.76)
Polycentropidae				0.61 (1.46)			
Polycentropus sp.	33.88 (105.20)	7.95 (5.96)		0.56 (1.53)	0.05 (0.17)		
Psychodidae			0.04 (0.08)				
Rhizelmis sp.				0.00 (0.00)		0.29 (0.62)	
Rhyacophila acropedes	35.16 (49.13)	14.40 (12.74)	8.66 (16.18)	1.20 (3.81)	0.28 (0.88)		
Serratella tibialis	21.75 (36.92)	17.63 (15.30)	12.11 (8.29)	5.55 (9.30)	1.87 (4.76)	1.92 (4.55)	11.77 (23.15)
Stratiomys sp.				0.93 (2.93)			
Timpanoga sp.					0.00 (0.00)		
Trichoptera			0.01 (0.03)		0.14 (0.38)	1.14 (3.47)	0.03 (0.10)
"A"				0.04 (0.12)	0.69 (1.21)	0.05 (0.15)	
"B"				0.08 (0.18)	1.38 (2.74)	0.03 (0.09)	
"C"				0.06 (0.19)	0.47 (1.27)		

Appendix 2. (continued)

FFG/Species	Cliff Creek	Beaver Creek	Ramey Creek	Rush Creek	Big/Coxey	Big/Rush	Big/Gorge
adult	0.65 (1.37)						
pupae	22.30 (49.43)	17.91 (37.75)	3.14 (9.94)				
Tricorythodes sp.						0.06 (0.18)	0.22 (0.68)
Scrapers							
Baetis sp.							
alexandii						1.54 (2.37)	
bicaudatus				20.65 (21.30)		2.13 (6.74)	1.00 (3.16)
intermedius				16.85 (16.11)	0.20 (0.64)		1.07 (2.83)
parvus	25.87 (42.67)	56.89 (38.64)					
sp. adult		0.53 (1.69)					
tricaudatus			81.33 (44.82)	12.60 (21.73)	14.49 (14.88)	20.93 (15.21)	30.91 (45.79)
Blepharicaria				3.34 (7.88)			
Caudatella hystrix			0.95 (2.04)				
Cinygmula sp.	86.22 (62.65)	33.90 (22.67)	27.86 (26.46)	19.54 (30.76)	3.93 (5.30)	0.75 (1.03)	0.96 (1.46)
Deuterophlebia sp.		0.28 (0.87)					
Dioptopsis sp.							0.22 (0.58)
Drunella sp.				0.24 (0.76)			0.11 (0.36)
colordensis	90.71 (77.24)	5.66 (10.55)	36.22 (52.72)				
doddsi	2.40 (2.01)	1.03 (0.89)	20.78 (61.07)	2.17 (4.22)	0.13 (0.28)		
spinifera		28.66 (49.62)	4.52 (13.60)	2.06 (6.29)			
Dactylolabes sp.				0.12 (0.39)			
Deuterophlebia sp.				0.09 (0.27)			
Epeorus sp.					0.02 (0.07)	2.17 (6.85)	
albertae					0.03 (0.09)	4.41 (12.25)	1.87 (2.70)
deceptivus			17.86 (13.11)	1.97 (4.22)		0.09 (0.27)	
longimanus	14.51 (29.27)	58.66 (53.65)	22.01 (22.97)	10.03 (16.44)		5.94 (13.75)	19.22 (23.62)
Ephemerella sp.					0.04 (0.08)		
aurivilli						10.90 (15.26)	
heterocaudatus		0.44 (1.39)					
inermis		4.32 (13.51)	0.93 (0.95)	3.39 (10.71)	1.49 (4.71)	0.03 (0.10)	0.07 (0.22)
margarita				6.99 (10.47)			3.07 (9.70)
Glossosoma sp.	0.83 (1.32)		0.01 (0.04)	0.36 (0.63)		0.19 (0.28)	0.24 (0.53)
Gordiidae				0.92 (2.91)			
Helichus sp. adult						2.03 (3.86)	
Heptageniidae			2.75 (1.94)	0.65 (2.05)		0.04 (0.12)	1.10 (3.48)

ppendix 2. (continued)

FG/Species	Cliff Creek	Beaver Creek	Ramey Creek	Rush Creek	Big/Coxey	Big/Rush	Big/Gorge
ydroptila sp.				21.42 (27.40)	0.97 (1.33)	0.66 (0.77)	5.91 (5.73)
pupae				0.24 (0.76)		0.45 (1.43)	0.15 (0.49)
ymnae						3.91 (4.98)	174.48 (349.67)
eophylax sp.	9.98 (20.24)			4.31 (13.61)			
logophlebodes sp.			0.20 (0.38)				
hilourons californicus				0.89 (2.82)			
hysidae						6.29 (13.09)	70.00 (126.42)
hithrogena sp.			6.16 (6.22)	3.17 (10.01)		0.50 (0.66)	0.04 (0.12)
adpole			23.91 (75.59)				
aenyopterygidae				0.03 (0.09)			
hredders							
lloperla sp.	76.04 (75.87)	6.39 (7.50)	8.47 (9.58)	7.99 (9.02)	5.53 (11.31)	5.93 (5.37)	3.75 (4.05)
apnia sp.	1.57 (4.64)			0.15 (0.47)			0.15 (0.48)
lostoeca sp.	0.63 (1.99)						
ara				2.08 (3.92)			
imnephila sp.				3.09 (4.29)			
imnephilus sp.				25.38 (53.58)			
imnephilidae			0.37 (0.41)			0.07 (0.16)	
imnephilidae pupae			1.04 (3.30)				
licrasema sp.	0.75 (1.60)	0.19 (0.41)	1.44 (3.57)		0.39 (1.24)		
lemoura sp.			0.89 (0.84)	0.07 (0.23)			
teronarcella sp.				1.40 (3.20)			0.25 (0.78)
teronarcys californicus				0.54 (1.70)	3.17 (2.38)	1.11 (1.92)	1.15 (1.86)
ipula sp.	119.23 (264.15)	0.11 (0.34)		1.51 (3.26)			0.04 (0.12)
isoka cataractae			0.07 (0.22)				
oroperla brevis	0.15 (0.48)		2.19 (6.92)				
apada sp.				0.62 (1.08)	0.07 (0.21)	0.10 (0.32)	
cinctipes					0.05 (0.15)		
columbiana							
oregonesis	7.25 (18.10)	5.29 (3.77)	4.61 (4.69)	0.65 (1.28)			
ilterers							
rctopsyche sp.		1.02 (1.13)					
grandis	7.57 (23.93)	93.03 (184.75)		20.83 (36.36)	15.84 (44.58)	0.03 (0.09)	1.39 (3.19)
rachycentrus sp.		5.50 (11.25)	4.38 (9.35)	192.57 (505.46)	37.13 (57.16)	5.63 (12.53)	3.08 (7.78)

Appendix 2. (continued)

FFG/Species	Cliff Creek	Beaver Creek	Ramey Creek	Rush Creek	Big/Coxey	Big/Rush	Big/Gorge
pupae				3.24 (10.25)			
Cladocera			0.85 (2.08)				
Dolophilodes sp.						0.08 (0.26)	
Hydropsyche sp.		0.34 (0.67)	1.08 (3.40)	28.66 (64.10)	0.77 (1.31)	13.04 (13.08)	42.18 (77.83)
Hydropsychidae				0.63 (1.35)		0.40 (0.67)	2.74 (5.57)
Ogiloplectrum sp.				19.7 (39.9)			2.27 (7.19)
Ostracoda	5.34 (16.90)	0.27 (0.73)		0.60 (1.56)		0.03 (0.09)	
Parapsyche sp.			4.22 (3.85)				
elis			146.54 (204.79)				0.39 (1.24)
Simulium sp.	5.98 (9.84)	16.23 (34.65)	1.07 (1.75)	149.79 (318.67)	0.70 (1.15)	0.24 (0.21)	16.07 (33.25)
adult							
pupae		0.27 (0.87)					0.57 (1.79)
Miners							
Chironomidae	9.63 (10.55)	45.79 (47.89)	14.65 (10.33)	92.49 (69.02)	47.48 (31.90)	42.59 (20.07)	125.15 (97.96)
adult		0.22 (0.71)	0.15 (0.32)			0.55 (0.72)	
pupae	0.29 (0.41)	1.79 (1.39)	2.48 (1.64)	4.25 (4.39)	0.41 (1.29)	2.86 (3.51)	2.90 (8.64)
Lumbriculus sp.	66.41 (143.22)				12.24 (38.70)		
Tubificidae	50.54 (73.81)	21.72 (22.05)	101.15 (78.22)	29.50 (52.16)	4.56 (4.62)	0.01 (0.04)	7.15 (7.81)
Others							
Ceraclea sp.							0.22 (0.69)
Helichus adult				0.24 (0.76)			
Molanna sp.		2.23 (5.32)		4.14 (7.43)			3.72 (10.90)
Pupae, unknown				1.15 (3.62)			
Pseudoscorpion	0.00 (0.00)						
Tadpole	195.47 (618.14)						
Tres sp.							0.09 (0.29)
Terrestrials	3.25 (7.86)	3.83 (3.00)	8.96 (13.73)	2.89 (5.05)		0.10 (0.20)	
Normaldia			11.51 (22.93)				